1960

Cytogenetic Relationships Between Cultivated Rice and Other Diploid Species of Oryza.

Birdie Pu-sheng Yeh
Louisiana State University and Agricultural & Mechanical College

Parent species or hybrids	Average no. per cell		Total cell examined	No. cell with the following number of univalents							
	rod-shaped bivalents	loosely held bivalents		2	4	6	8-14	16-22	24	total	%
12.	4.04	0.68	488	2	0	0	0	0	0	2	0.40
13.	3.72	0.36	524	2	0	0	0	0	0	2	0.38
14.	3.91	0.63	600	9	0	0	0	0	0	9	1.50
15.	3.79	0.72	556	10	0	0	0	0	0	10	1.79
16.	6.27	0.40	560	5	2	0	0	0	0	7	1.25
E. Cross between O. sativa and O. perennis var. barthii.											
17.	3.82	1.39	467	17	1	0	3	0	0	21	4.49
F. Cross between O. sativa var. formosana and O. perennis var.cubensis.											
18.	3.32	0.35	408	2	0	0	0	0	0	2	0.49
G. Crosses between O. balunga and O. perennis.											
19.	-	-	-	-	-	-	-	-	-	-	-
20.	-	-	-	-	-	-	-	-	-	-	-
H. Cross between O. perennis var. cubensis and O. perennis var. barthii.											
21.	3.34	0.31	515	0	1	0	0	0	0	1	0.19

Parental species or hybrids	Average no. per cell		Total cell examined	No. cell with the following number of univalents							
	rod-shaped bivalents	loosely held bivalents		2	4	6	8-14	16-22	24	total	%
I. Crosses between O. glaberrima varieties.											
22.	1.60	0.05	388	0	0	0	0	0	0	0	0.00
23.	3.84	0.52	436	7	2	0	0	0	0	9	2.06
J. Crosses between O. sativa and O. glaberrima.											
24.	2.15	2.83	278	57	21	4	40	31	20	173	62.23
25.	1.18	1.71	381	36	51	3	8	40	149	287	75.32
26.	2.61	2.55	419	95	70	3	9	3	8	188	44.86
27.	3.33	1.78	419	128	51	2	1	5	11	198	47.25
28.	3.96	1.33	544	114	22	0	6	1	0	143	26.28
29.	3.59	1.13	419	94	33	3	0	3	23	156	37.23
30.	0.82	1.00	346	35	9	2	2	5	129	182	52.60
K. Cross between O. balunga and O. glaberrima.											
31.	1.90	1.52	401	83	20	0	0	0	0	103	25.68
L. Crosses between O. glaberrima and O. breviligulata.											
32.	4.78	0.79	305	8	0	0	0	0	0	8	2.62

Parental species or hybrids	Average no. per cell: rod-shaped bivalents	Average no. per cell: loosely held bivalents	Total cell examined	No. cell with the following number of univalents: 2	4	6	8-14	16-22	24	total	%
33.	4.33	0.40	306	5	0	0	0	0	0	5	1.63
M. Crosses between O. glaberrima and O. stapfii.											
34.	0.27	0.29	230	0	0	0	0	0	0	0	0.00
35.	2.34	0.12	408	0	0	0	0	0	0	0	0.00
N. Crosses between O. sativa and O. breviligulata.											
36.	1.49	0.76	467	27	4	0	1	0	0	32	6.85
37.	2.75	2.33	408	65	37	4	12	6	27	151	37.00
38.	2.03	1.60	435	43	56	0	12	11	119	241	55.40
O. Crosses between O. sativa and O. stapfii.											
*39.	4.38	1.21	413	106	13	1	1	0	0	121	29.30
40.	3.02	3.33	408	84	64	6	8	3	1	166	40.68
P. Cross between O. sativa and O. officinalis.											
**41.	-	-	14	cells were found to contain 24, 28, 29, 32 and 69 bodies each.							100.00

* one cell was found to contain a quadrivalent (ring of 4) and 10 bivalents.
** somatic tissue showed 2n = 36 chromosomes.

Table II. Irregularities at anaphase I and telophase I of meiosis and degree of fertility in parental species and F_1 generation of interspecific hybrids.

Parental species or hybrids	Anaphase I			Telophase I		Fertility	
	Total cells examined	Abnormal cells no.	Abnormal cells %	Total cells examined	% cells abnormal	Stainable pollen(%)	Seed set (%)
O. sativa	1134	0	0.0	1304	0.0	92.6	-
O. sativa var. fatua	-	-	-	-	-	78.7	-
O. sativa var. formosana	-	-	-	-	-	85.5	-
O. balunga	507	0	0.0	400	0.0	95.7	-
O. perennis var. cubensis	-	-	-	-	-	-	-
O. perennis var. barthii	-	-	-	-	-	-	-
O. glaberrima	707	0	0.0	783	0.0	91.3	-
O. breviligulata	211	0	0.0	400	0.0	84.0	-
O. stapfii	188	0	0.0	340	0.0	83.7	-
O. officinalis	22	0	0.0	23	4.3	31.0	-
A. Crosses between O. sativa and O. sativa var. fatua.							
1.	411	0	0.0	300	0.0	90.3	83.4

Parental species or hybrids	Anaphase I			Telophase I		Fertility	
	Total cells examined	Abnormal cells		Total cells examined	% cells abnormal	Stainable pollen(%)	Seed set (%)
		no.	%				
2.	403	0	0.0	525	0.0	67.3	60.5
3.	239	0	0.0	252	0.0	79.3	86.9
B. Cross between O. sativa and O. sativa var. formosana.							
4.	327	0	0.0	400	0.0	93.6	64.0
C. Crosses between O. sativa and O. balunga.							
5.	474	0	0.0	425	0.0	99.9	94.8
6.	58	0	0.0	225	0.0	78.4	-
7.	511	0	0.0	350	0.0	78.0	-
8.	367	0	0.0	300	0.0	96.6	-
9.	361	1	0.27	375	0.0	96.0	-
D. Crosses between O. sativa and O. perennis var. cubensis.							
10.	387	1	0.25	592	0.0	8.2	0.0
11.	211	1	0.47	314	0.0	14.2	0.0
12.	398	3	0.75	561	0.0	11.4	0.0
13.	723	7	0.96	1029	0.0	14.9	0.0

Parental species or hybrids	Anaphase I			Telophase I		Fertility	
	Total cells examined	Abnormal cells		Total cells examined	% cells abnormal	Stainable pollen(%)	Seed set (%)
		no.	%				
14.	340	3	0.88	540	0.0	12.8	0.0
15.	194	2	1.03	375	0.0	16.2	0.0
16.	242	1	0.41	490	0.0	12.5	0.0
E. Cross between O. sativa and O. perennis var. barthii.							
17.	317	7	2.21	315	0.0	70.4	5.1
F. Cross between O. sativa var. formosana and O. perennis var. cubensis.							
18.	595	0	0.0	475	0.0	20.0	2.0
G. Crosses between O. balunga and O. perennis.							
19.	-	-	-	-	-	-	-
20.	-	-	-	-	-	-	-
H. Cross between O. perennis var. cubensis and O. perennis var. barthii.							
21.	228	11	4.82	466	0.0	100.0	-
I. Crosses between O. glaberrima varieties.							
22.	213	0	0.0	351	0.0	93.5	-
23.	228	0	0.0	326	0.0	92.3	-

Parental species or hybrids	Anaphase I			Telophase I		Fertility	
	Total cells examined	Abnormal cells no.	%	Total cells examined	% cells abnormal	Stainable pollen(%)	Seed set (%)
J. Crosses between O. sativa and O. glaberrima.							
24.	40	18	45.0	33	0.0	0.3	0.0
25.	87	35	40.2	119	0.0	0.2	0.0
26.	310	19	6.1	402	0.5	0.0	0.0
27.	87	3	3.4	233	1.3	5.9	0.0
28.	148	11	7.4	216	0.0	1.8	0.0
29.	143	11	7.7	230	1.3	3.6	0.0
30.	69	10	14.5	273	0.4	5.9	0.0
K. Cross between O. balunga and O. glaberrima.							
31.	396	2	0.5	350	0.0	4.5	0.0
L. Crosses between O. glaberrima and O. breviligulata.							
32.	67	0	0.0	197	0.0	84.0	52.3
33.	146	0	0.0	234	0.0	70.2	54.6
M. Crosses between O. glaberrima and O. stapfii.							
34.	152	0	0.0	450	0.0	99.8	-
35.	551	0	0.0	500	0.0	94.2	83.9

Parental species or hybrids	Anaphase I			Telophase I		Fertility	
	Total cells examined	Abnormal cells no.	%	Total cells examined	% cells abnormal	Stainable Pollen(%)	Seed set (%)
N. Crosses between O. sativa and O. breviligulata.							
36.	154	9	5.8	185	1.6	0.4	0.0
37.	120	6	5.0	281	2.1	11.7	0.05
38.	106	11	10.4	356	1.7	51.9*	0.0
O. Crosses between O. sativa and O. stapfii.							
39.	341	8	2.3	398	0.0	0.5	0.0
40.	356	5	1.4	269	0.7	0.0	0.0
P. Cross between O. sativa and O. officinalis.							
41.	3	3	100.0	-	-	-	-

* Pollen grain only slightly stained.

In appearence, the F_1 plants resembled O. sativa var. fatua more closely in such characteristics as color of stigma, color of seed coat, awn condition, color of leaves and stems and shattering of grains.

In the cytological studies of diakinesis and MI for the three crosses, approximately 400 PMCs per cross were examined. The frequency of rod-shaped bivalents per cell ranged from 3.76 to 4.50 and the frequency of loosely held bivalents varied from 0.45 to 1.22 per cell among the three crosses. As shown in Table I, both of these conditions involving degree of crossing over in the chromosomes were somewhat more frequent in the O. sativa X O. sativa var. fatua hybrids than in the homozygous cultivated varieties of O. sativa studied.

The percentage of cells having univalents at diakinesis and MI varied from 2.35 to 11.02 for the three crosses. In one of the crosses (hybrid No. 3), no PMC was found with more than two univalents. In another cross (hybrid No. 1), PMC with as many as four univalents were observed. In a third cross (hybrid No. 2), there were two PMCs with as many as 8-14 univalents, this is the same cross in which a very high percentage (11.02) of cells contained univalents. All of the hybrids showed a considerably higher frequency of cells with univalents than was found in the O. sativa parent varieties, in which three cells with two univalents each were found among 1458 cells examined---a frequency of only 0.2 %.

As indicated in Table II, no abnormalities were found in AI or TI for any of the three hybrids.

The percentage of pollen stainable in aceto-carmine ranged from

67.3 to 90.3 in the hybrids. The percentages of florets setting seed for these hybrids varied from 60.5 to 86.9. The fertility results suggest that one of the hybrids (hybrid No. 1) was completely fertile while the other two showed a low degree of sterility.

Yao, et al.(1958) reported that up to 8 % of MI cells contained univalents in hybrids between varieties of cultivated rice, and also reported a higher frequency of rod bivalents in some of these hybrids than in homozygous varieties studied. Thus, although the higher frequency of rod-shaped and loosely held bivalents and of univalents found in the hybrids in the present study may indicate some degree of chromosome differentiation between O. sativa var. fatua and O. sativa, this differentiation does not appear to be any greater than that present among varieties of O. sativa itself. Furthermore, the slight degree of sterility found in two of the three hybrids does not indicate that O. sativa var. fatua and O. sativa should be placed in separate species. Degrees of sterility exceeding those found in hybrids No. 2 and 3 have been found commonly in crosses between distantly related cultivated varieties of O. sativa.

On the basis of results obtained from this experiment, the author concludes that O. sativa var. fatua is very closely related to O. sativa and agrees with the previous classification of this form as a botanical variety of O. sativa. This conclusion is based on the close morphological similarities between O. sativa and O. sativa var. fatua, the moderately high to complete fertility of hybrids between these two forms and the fact that chromosome be-

havior in meiosis was as regular as that reported in intervarietal hybrids of O. sativa. The author feels that there may have been some differentiation of the chromosomes in these two forms, but that this differentiation is no greater than that occurring within O. sativa between such types as indica and japonica.

(B) Cross between O. sativa and O. sativa var. formosana:-

One cross of this type between the cultivated variety Colusa of O. sativa and O. sativa var. formosana was included in the study. The wild Formosan form with large anthers and an abundance of pollen was used as the male parent.

The percentage of pollinated florets which set seeds in making this cross was 32.7 and the F_1 seeds were all well developed. Thus, it was the author's experience that this cross is fully as easy to make as crosses between cultivated varieties of O. sativa.

In general morphology, plants of the F_1 were more similar to var. formosana than to the O. sativa parent. Anthocyanin developed in leaves and stems of the F_1 in a manner resembling var. formosana. In addition, the dark grey hull color of mature spikelets and the awnletted condition of the spikelets shown by the F_1 indicated that these characters of the var. formosana parent are dominant.

A total of 408 PMCs were examined for the cytological study of chromosome behavior in diakinesis and MI of the F_1. The frequencies of rod-shaped and loosely held bivalents per cell were 3.37 and 0.51, respectively. These values are slightly higher than those found in homozygous varieties of O. sativa, as indicated in Table I, but were

no higher than those found in hybrids of O. sativa with O. sativa var. fatua.

Among the 408 cells in diakinesis and MI which were studied, five cells were found to contain two univalents each and no cells with more than two univalents were observed in this hybrid. This gives a percentage of 1.2 cells with univalents, again a slightly higher frequency than found in the O. sativa parent.

As shown in Table II, no abnormalities were found at AI and TI in this hybrid.

The percentage of pollen of the F_1 which was stainable in aceto-carmine was 93.6, a value which indicates that the hybrid was probably completely fertile. In fact, this figure is noticeably higher than the percentage of stainable pollen obtained from the var. formosana parent (85.5) but is about the same as found in cultivated varieties of O. sativa. The percentage of florets on F_1 plants which set seed was 64.0. This is low in view of the high percentage of apparent normal pollen. However, as described in the previous section, var. formosana showed a somewhat low percentage of seed setting although the percentage of stainable pollen was high. Thus, the tendency of the hybrid to set fewer seed than expected from the data on stainable pollen is similar to the behavior of var. formosana.

On the basis of the results obtained from this cross, the author concludes that O. sativa var. formosana is a wild form very closely related to O. sativa and should be considered as a botanical variety of O. sativa. As in the previous case of O. sativa

var. fatua, this conclusion is based on strong similarity in morphological characters, high fertility of the hybrid and regularity of chromosome behavior in meiosis. Although it has been suggested by some workers that this wild form found in Formosa should be classified as O. sativa var. fatua, the author feels that it does not fit this form because of its semi-procumbent and perennial growth habit. For this reason, the name O. sativa var. formosana is adopted provisionally.

(C) Crosses between O. sativa and O. balunga:-

Five varieties of O. sativa (Carolina Gold, Fortuna, Colusa, Calrose and Nato) were hybridized with the wild perennial species designated O. balunga in these studies. The latter was used as the male parent for all crosses of this type except for one cross (hybrid No. 5) in which the cultivated variety Carolina Gold was employed as the pollen parent.

The percentage of seed set from pollinated florets ranged from 1.5 to 40.0 with a mean of 10.3 %. Although this mean seed set is lower than that obtained in the previous two types of crosses and that resulting from crosses between cultivated varieties within O. sativa, this cross proved rather easy to make, the readiness being demonstrated by the fact that the highest seed set for a cross was up to 40 % in this study. No incompatibility appeared to exist between these two forms in this respect.

In general morphology and growth habit, plants of the F_1 varied from erect to semi-procumbent in different crosses but all of them

showed the perennial habit and had a strong tendency to root at the lower nodes of the stem. Tillers developed continuously on the F_1 plants. Stems generally were large in diameter. Slight red pigment developed in leaf sheath and stem. The ligule is long, colorless to pink, acute and cleft at the tip. The panicle is lax, branches opening to an almost 90° angle from the main axis when the grains approach maturity. The length of the spikelets varied among the crosses from medium to long. The surface of lemma and palea is hairy. The awns are long and red in color. The hulls and awns turn black when the spikelets mature. Grains shatter easily. The sterile lemmas are short and lanceolate in shape. Stigma is purple. Anthers are yellow, long, but intermediate between parents (not quite as long as those of the O. balunga parent). The seed coat color is red.

When compared with both parents, the general appearence of the F_1 plants is intermediate except in such characters as the perennial habit, the lax panicle and color of the hulls, stigma and seed coat, which are similar to O. balunga(Photo. 1 and 2).

In the cytological studies of diakinesis and MI for the five crosses, 300-400 PMCs per cross were examined. The frequency of rod-shaped bivalents per cell ranged from 2.04 to 3.36 and the frequency of loosely held bivalents varied from 0.56 to 1.74 per cell among the five crosses. As shown in Table I, these frequencies as a whole for all crosses of this type were slightly higher than those obtained in homozygous varieties of O. sativa but were not any higher than those found in the previous two types of crosses.

The percentage of cells containing univalents at diakinesis and

Photo. 1. Mature plant of O. balunga (O. perennis var. balunga). Note procumbent growth habit.

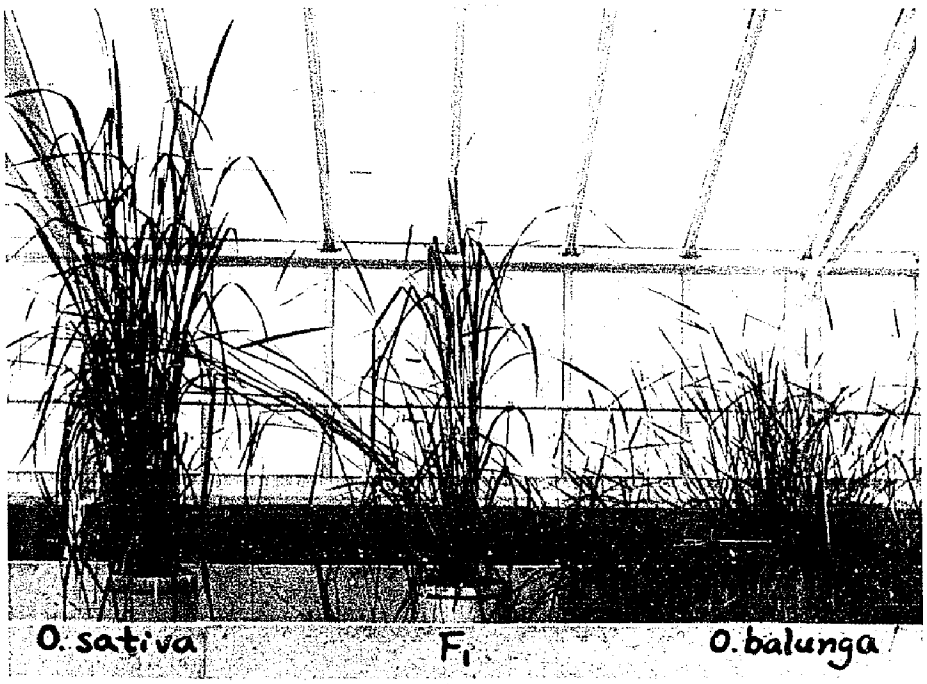

Photo. 2. Mature plants of O. sativa (Carolina Gold), O. balunga (O. perennis var. balunga) and the F_1 hybrid.

MI varied from 0.0 to 5.13 among the five crosses. In one of the crosses (hybrid No. 5), no cell with univalents was observed in 419 cells examined. In two of the crosses (hybrids No. 6 & 7), no PMC was found with more than two univalents. In the other two crosses (hybrids No. 8 & 9), one cell with four univalents was found in each cross in addition to a somewhat higher frequency of cells with two univalents. Except for hybrid No. 5, all of the crosses showed a slightly higher percentage of cells having univalents than in homozygous cultivated varieties of O. sativa. However, as a whole, the values obtained from this type of cross were not appreciably higher than that in the cross between O. sativa and O. sativa var. formosana and certainly were somewhat lower than what was found in the crosses between O. sativa and O. sativa var. fatua. As indicated in Table I, in most of the cells examined, except the few with univalents, the chromosome behavior was regular with the formation of 12 bivalents (Photo. 3 & 4). A photomicrograph showing four univalents and 10 bivalents at diakinesis in one of the F_1 plants is also presented here (Photo. 5).

No abnormalities were found at AI and TI in four of the five hybrids. In hybrid No. 9. one cell at AI was found to have two lagging chromosomes undergoing equational division while 11 chromosomes had already moved to each pole. This gives a percentage of 0.27 abnormal cell in a total of 361 AI PMCs examined for hybrid No. 9.

The percentage of pollen stainable in aceto-carmine ranged from 78.0 to 99.9 for the five crosses, indicating high to complete

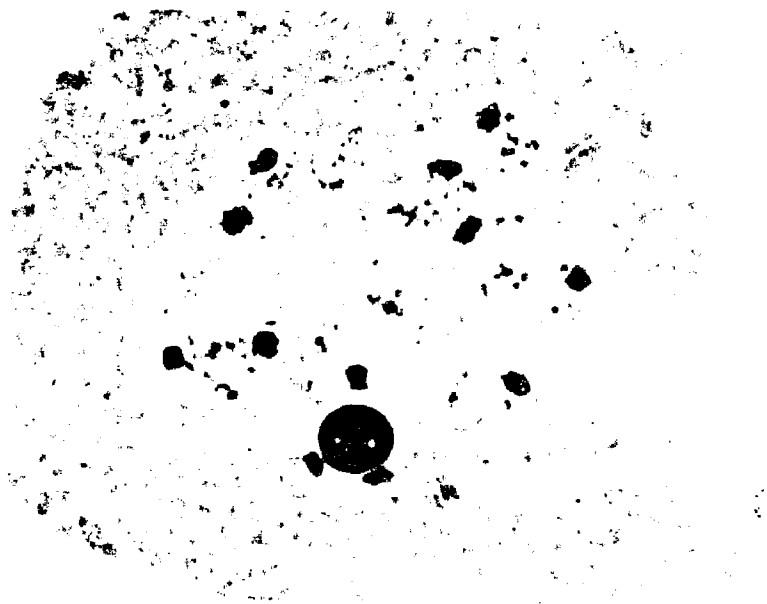

Photo. 3. Late diakinesis in the F_1 plant of O. sativa (Colusa) X O. balunga (O. perennis var. balunga) showing the 12 normal bivalents.

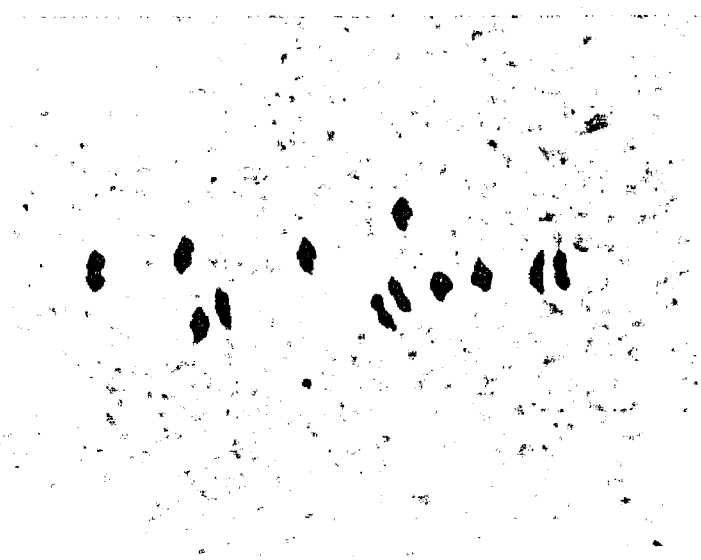

Photo. 4. Metaphase I in the F_1 plant of O. sativa (Colusa) X O. balunga (O. perennis var. balunga) showing the 12 bivalents. Several of the bivalents are rod-shaped.

Photo. 5. Late diakinesis in the F_1 plant of O. sativa (Nato) X O. balunga (O. perennis var. balunga) showing 10 bivalents and 4 univalents.

fertility in these crosses. At the time of writing this dissertation, the F_1 plants had not reached the stage necessary for measuring seed set, except for one cross (hybrid No. 5) which was made in a previous season. It showed an almost complete fertility of 94.8 % florets setting seed.

From the results obtained in the study of crosses between varieties of O. sativa and the wild type O. balunga, such as the ease of making the crosses, the regular behavior of chromosomes during meiosis and the high to complete fertility in F_1 plants, the author concludes that O. balunga is very closely related to O. sativa and the cytogenetic relationship between the two is no more distant than the relationship between O. sativa and the two botanical varieties, var. fatua and var. formosana presented previously. However, in view of the great differences in morphology between O. sativa and O. balunga and the distinct perennial and procumbent growth habit of the latter, the author feels that O. balunga should be considered as a separate species from O. sativa. For this reason, as indicated in the previous section, the name O. balunga has been adopted provisionally. The reasons why the author feels that this form should also be recognized as a separate species from O. perennis will be presented later in the dissertation after all of the results from other hybrids have been discussed.

The author is of the opinion that O. balunga is probably the ancestral form of our cultivated rice, O. sativa. Further evidence from which this opinion was reached will be presented in a later section.

(D) Crosses between O. sativa and O. perennis var. cubensis:-

Seven crosses of this type were made in 1957. The cultivated varieties of O. sativa involved in these crosses were Nira, Nato, Calrose, Asahi, Fortuna, Carolina Gold and Improved Blue Rose. O. perennis var. cubensis was employed as the pollen parent for all crosses.

An average of 16.5 % of pollinated florets setting seed in making this type of cross was obtained and the development of the F_1 seed appeared to be normal. Although the percentage of seed set from pollinated florets was not very low, it was the author's experience that crosses between these two forms were not as easy to make as for the previously reported three types of crosses. A large number of florets, more than 700, were pollinated in an attempt to get sufficient F_1 seed and plants for the study.

In appearence, the F_1 plants resembled O. perennis var. cubensis more closely in such characters as anthocyanin development in the leaf sheath, color of stigma, awn condition and shattering of the spikelets. As to the growth habit, the F_1 plants all showed the same characteristics as the perennis parent. They were perennial and required short-days for flowering. They also resembled O. perennis var. cubensis in that they did not form stems with nodes until panicle initiation was induced by short-day treatment. Until then, only leafy tissue was present in the plant.

Results from cytological studies of meiosis in the F_1 plants showed that at MI the frequency of rod-shaped bivalents per cell ranged from 3.19 to 6.27 and the frequency of loosely held bivalents

varied from 0.36 to 0.72 per cell among the seven crosses studied. These frequencies proved to be higher than those observed in homozygous varieties of O. sativa and the occurrence of rod-shaped bivalents appeared to be more frequent than in the previous types of crosses, i.e., crosses of O. sativa with O. sativa var. formosana and O. balunga, but not appreciably higher than in the crosses between O. sativa and O. sativa var. fatua.

At diakinesis and MI, the percentage of cells having univalents ranged from 0.0 to 1.79 for the seven crosses. Only in two crosses (hybrids No. 10 & 16) were cells found which contained more than two univalents. In hybrid No. 10, one cell containing six univalents was observed and in hybrid No. 16 there were two cells with four univalents. No cells having univalents were found in hybrid No. 11. In the rest of the crosses not more than two univalents per cell were observed although the frequency of such cells varied (Photo. 6). This kind of abnormality was somewhat more frequent than in the homozygous varieties of O. sativa but the values are not any higher than those obtained in the previously reported three types of crosses.

At AI, as indicated in Table II, certain abnormalities were observed in all of the crosses with the percentage of abnormal cells ranging from 0.25 to 1.03. As shown in Photo. 7, a cell at AI in hybrid No. 13 contained 11 chromosomes at each pole and a bridge plus a fragment. This type of abnormality in the F_1 apparently was due to the heterozygous condition of a paracentric inversion. Abnormalities observed in other hybrids all belong to

Photo. 6. Metaphase I in the F_1 plant of O. sativa (Nira) X O. perennis var. cubensis showing 11 bivalents and 2 univalents.

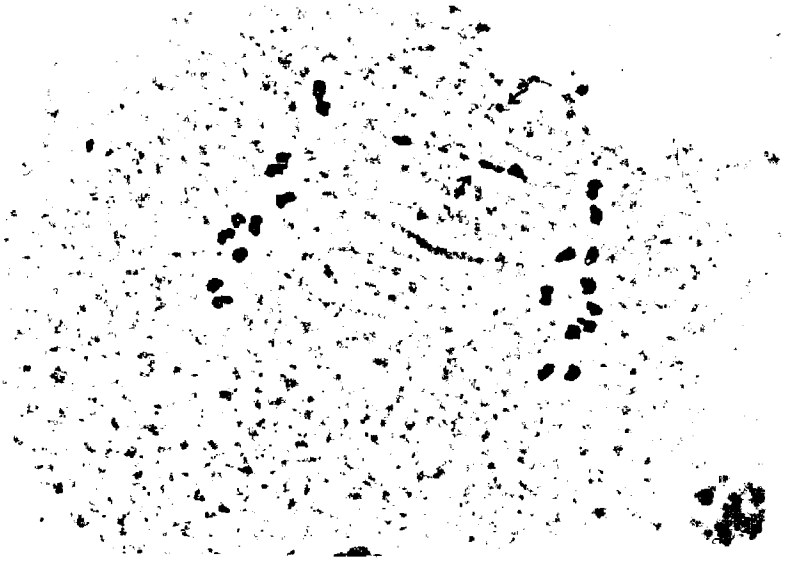

Photo. 7. Anaphase I in the F_1 plant of O. sativa X O. perennis var. cubensis showing bridge and fragment.

one catagory which showed 11 chromosomes at each pole and a lagging unseparated bivalent. This consistent, though infrequent, occurrence of abnormalities at AI seemed to indicate that there is some degree of chromosome differentiation between the two forms involved in the crosses. No abnormalities were found at TI for any of the seven hybrids.

The percentage of pollen stainable in aceto-carmine varied from 8.2 to 16.2 among the seven crosses. However, no seed was set in several thousands florets examined. The low percentage of stainable pollen and the complete self sterility shown by the seed set data differentiate this type of cross from all of the previously reported types.

The homology shown in chromosome behavior at diakinesis and MI suggests that O. perennis var. cubensis is a wild form closely related to O. sativa. However, the abnormalities found at AI and the complete sterility of F_1 plants indicate that the relationship between this perennial wild form and O. sativa is not as close as between O. sativa and the botanical varieties, var. fatua and var. formosana, or between O. sativa and O. balunga. Furthermore, differences in geographical distribution, morphological characters and growth habit also distinguish O. perennis var. cubensis from O. sativa. Thus, the author concludes that there is no doubt that O. perennis var. cubensis is a separate species distinct from O. sativa but related to the latter.

Based on the extremely close relationship observed between O. sativa and O. balunga and the more distant relationship between

O. sativa and O. perennis var. cubensis, primarily shown in the the chromosome behavior and fertility of the F_1 plants, it can be inferred indirectly that O. balunga should be considered as a separate species from O. perennis. It is for this reason that the author adopted the specific status and the name O. balunga for the wild form found in India instead of accepting it as a variety of O. perennis as suggested by Sampath and Govindaswami (1958).

(E) Cross between O. sativa and O. perennis var. barthii:-

Several cultivated varieties of O. sativa were used as the seed parent in attempts at hybridization between O. sativa and O. perennis var. barthii. However, F_1 seed was obtained from only one combination, between the cultivated variety Calrose and this wild African form of O. perennis. From a large number of florets (464) pollinated in this combination, only one germinable seed was obtained, which gives a percentage of 0.21. This single seed was not well developed, but fortunately the author was able to obtain a normal F_1 plant from it for the study of this type of cross.

The general morphology of the single F_1 plant was generally intermediate between the two parents. However, in some characters, such as the dark purple color of the stigma, the red colored long awns, shattering of the spikelets and the perennial growth habit, the F_1 resembled the African wild form more closely, although the development of rhizomes in the F_1 plant was not as strong as in O. perennis var. barthii.

The study of meiosis showed that at diakinesis and MI the frequencies of rod-shaped and loosely held bivalents per cell were 3.82 and 1.39, respectively. These two kinds of possible abnormalities were slightly more frequent than in the homozygous varieties of O. sativa but the values are not higher than those obtained in the various previously reported types of hybrids.

Among the 467 PMCs examined at diakinesis and MI, 17 cells contained two univalents, one cell contained four univalents and three cells were found to have as many as 8-14 univalents. The percentage of total cells with various number of univalents was 4.49. This value is higher than those obtained in the cultivated varieties of O. sativa and in the O. sativa X O. perennis var. cubensis hybrid but similar to those found in the other three types of crosses described previously.

Five cells with 1-2 lagging chromosomes or 1 lagging bivalent plus two cells showing unequal disjunction (13 + 11) (Photo. 8) were observed at AI. This gives a total of 2.21 % cells with abnormalities among 317 PMCs examined. This value is higher than those obtained in all of the crosses preceding this one. All the PMCs examined at TI appeared to be normal.

The data on fertility of the F_1 plant in this cross were interesting though difficult to interpret. Despite the somewhat more irregular chromosome behavior of this hybrid than in the crosses of O. sativa with O. perennis var. cubensis, the percentage of stainable pollen was 70.4 and 5.1 percent of the florets set seed in contrast to the complete sterility in the O. sativa-O. perennis var. cubensis hybrids.

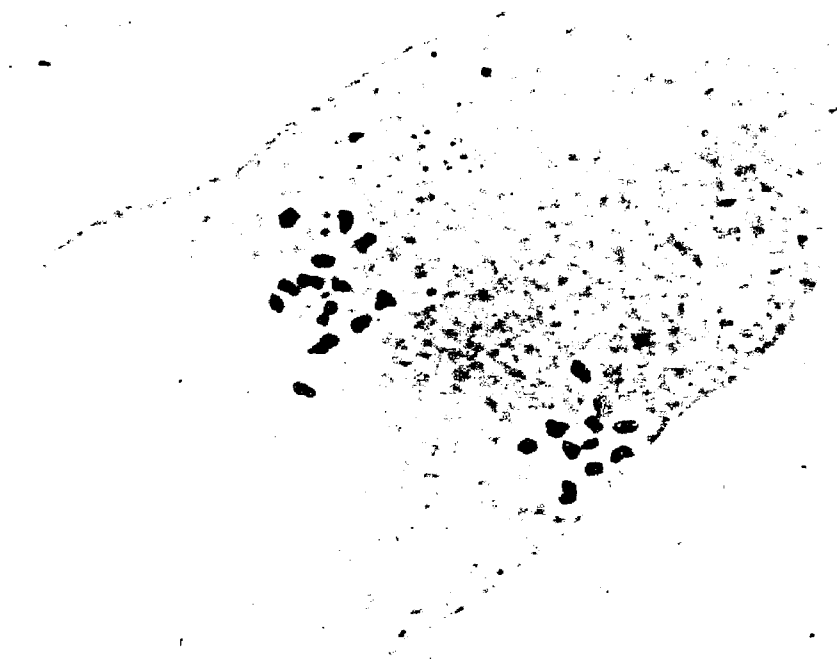

Photo. 8. Anaphase I in the F_1 plant of O. sativa (Calrose) X O. perennis var. barthii showing the unequal disjunction of the chromosomes. Note that 11 chromosomes are present at one pole and 13 at the other instead of 12 at each pole.

Based on the distinct differences in morphology and growth habit such as the strong development of rhizomes and the perennial habit, on the difficulty encountered in making the cross, on the chromosomal abnormalities occurring during meiosis I and the low fertility of the F_1 plant, it is concluded by the author that the wild African form involved in this cross is definitely a separate species distinct from O. sativa. However, the rather high degree of chromosome homology shown at diakinesis and MI and the occurrence of some degree of fertility in F_1 suggest that this species is also closely related to O. sativa, though certainly the relationship is not as close as that of O. sativa with O. sativa var. fatua, O. sativa var. formosana and O. balunga.

(F) Cross between O. sativa var. formosana and O. perennis var. cubensis:-

This cross was made by using the O. perennis form as the pollen parent. The percentage of pollinated florets which set seed when making the cross was 18.7. The F_1 seeds were well developed.

In general morphology, the F_1 plants resembled O. perennis var. cubensis more closely in such characters as the greater length of the spikelets (7-8 mm) and the long awns. In growth habit, the hybrid also resembled the perennis parent in such a way that no stem tissue formed in the plant before initiation of flowering was induced by artificial short-day treatment at Baton Rouge. The hybrid is perennial, a characteristic of both parental forms. However, it did not produce roots at the lower nodes of the stems as did the

Formosan form.

In the cytological studies of diakinesis and MI for this cross, 408 PMCs were examined. The frequencies of rod-shaped and loosely held bivalents per cell were 3.32 and 0.35, respectively. These values are similar or perhaps slightly lower than those observed in the hybrids between O. sativa and O. perennis var. cubensis.

The percentage of cells with univalents at diakinesis and MI was 0.49 with only two cells containing univalents and these having no more than two univalents each among the 408 PMCs examined. This frequency of cells with univalents is lower than in most of the hybrids between O. sativa and the Cuban form of O. perennis.

As indicated in Table II, no abnormalities were found in AI or TI for this hybrid.

The percentage of pollen stainable in aceto-carmine was 20.0. The percentage of florets setting seed for this hybrid was 2.0. Again, these values in fertility are slightly higher but similar to those found in the O. sativa X O. perennis var. cubensis hybrids.

The similarities in the results obtained from cytological and fertility studies of this cross and the crosses between O. sativa and O. perennis var. cubensis confirm that the relationship between O. perennis var. cubensis and O. sativa var. formosana is similar to that between the former and the cultivated rice, O. sativa. From this, the author concludes that, as expected, the Cuban form of O. perennis is closely related to both O. sativa and its botanical variety var. formosana.

(G) Crosses between O. balunga and O. perennis:-

For this type of combination, attempts were made to cross both the Cuban and African forms of the species O. perennis with O. balunga. These crosses were listed in 'Material and Methods' as hybrids No. 19 and 20. No. 19 is the hybrid between O. balunga and O. perennis var. cubensis from a cross using the latter as the seed parent while cross No. 20 is a combination between O. balunga and O. perennis var. barthii, with the latter as pollen parent.

The percentage of florets setting seed in making the No. 19 cross (O. perennis var. cubensis X O. balunga) was 56.6 and that for cross No. 20 (O. balunga X O. perennis var. barthii) was 31.8. However, F_1 seed from the latter cross were not well developed and most of them consisted only of the dried ovary wall without evidence of an embryo. No germination was obtained from seed of this cross.

In general morphology, the F_1 plants from the cross of O. perennis var. cubensis X O. balunga resembled O. balunga very closely in the vegetative stage of development. However, at the time of writing of this dissertation, the F_1 plants are still in the vegetative stage and have not yet produced any panicles despite short-day treatment. Consequently, no material was available for cytological and fertility studies.

(H) Cross between O. perennis var. cubensis and O. perennis var. barthii:-

The African form, var. barthii, was used as the male parent in this cross. The percentage of pollinated florets which set seed

was 3.75 and most of the seed were not normally developed, with a shrunken appearence. Among the few F_1 seeds obtained, only one seed proved germinable and from it a feeble plant developed that did not survive to maturity. Fortunately, however, material could be collected for cytological and pollen stainability studies before the plant died.

Since both parents resemble each other in their general morphology, except for the strong development of rhizomes in var. barthii, no special features were observed in the hybrid. Since the F_1 plant was weak, small and died before maturity, it was not possible to determine whether the plant was rhizomatous or not. However, the development of dark red pigment in the leaf sheath was noticeably stronger than in both parent forms.

Cytological studies of meiosis in the F_1 plant showed that the frequencies of rod-shaped and loosely held bivalents per cell were 3.34 and 0.31, respectively. These values are similar to or slightly lower than those found in hybrids between O. sativa and its botanical varieties.

Among the 515 PMCs examined at diakinesis and MI, only one cell was found to contain univalents, four in number, which gives a percentage of 0.19. This value is almost the same as that found in homozygous cultivated varieties within the species O. sativa, indicating a close kinship between these two forms of O. perennis.

As shown in Table II, 4.82 % of abnormal cells were found among 228 PMCs examined at AI. The only abnormality observed in these cells was the occurrence of one or two lagging bivalents due

to some kind of interference in the disjunction of the chromosomes which were paired before this stage. No abnormalities were found at TI, among 466 PMCs examined.

The percentage of pollen stainable in aceto-carmine was 100.00, indicating complete fertility. Unfortunately, however, as the plant died before reaching maturity, no seed set data could be obtained as supplimentary proof of such perfect fertility as indicated by the pollen stainability results.

Results from studies on this hybrid lead the author to conclude that the relationship between these two wild forms is very close. Consequently, the author agrees with the classification suggested by Chevalier (1932), that the African wild form should be grouped under the same species, O. perennis, with the American form found in the West Indies. These two forms are described in this dissertation under the designations O. perennis var. barthii and O. perennis var. cubensis.

The conclusion that the two forms are botanical varieties of one species was based on the similarities in morphology, the regular chromosome pairing shown at diakinesis and MI and the complete fertility indicated by the percentage of stainable pollen of the F_1 plant.. The relatively high frequency of abnormal cells observed at AI was probably due to some kind of genetic differentiation which occurred during the long separation of these two forms. The strongly rhizomatous condition and the complete self sterility shown at Baton Rouge in var. barthii are probably also indication of the occurrence of such genetic differentiation.

(I) Crosses between O. glaberrima varieties:-

Two crosses involving three cultivated varieties of O. glaberrima were included in the study of this type of hybrids, namely, Legheh X Kebleh (hybrid No. 22) and Legheh X Ekasa (hybrid No. 23).

The percentages of pollinated florets which set seed when making the crosses were 87.9 and 50.5 for crosses No. 22 and No. 23, respectively. The mean was 59.4 %. These crosses proved easy to make and the F_1 seed were all well developed.

The only noticeable difference in morphological feature in the parents is in the long sterile lemmas of the Ekasa variety. This condition was dominant over short lemmas.

As shown in Table I, from cytological studies, the frequencies of rod-shaped bivalents per cell were 1.60 and 3.84 for the two crosses and the frequencies of loosely held bivalents for the crosses were 0.05 and 0.52 per cell. As an average, these values are comparable to those found in homozygous cultivated varieties within the species O. sativa.

Cells with univalents were only observed in hybrid No. 23. In this hybrid, seven cells with two univalents and two cells containing four univalents were found among 436 PMCs examined. The percentage of total cells with univalents was 2.06. No cells were found having univalents in hybrid No. 22.

As indicated in Table II, no abnormalities were found at AI or TI for these two crosses.

The percentages of pollen stainable in aceto-carmine were 93.5 and 92.3 for hybrids No. 22 and No. 23, respectively. Although no

records were taken for the percentage of seed set, these F_1 plants proved to be fertile, as suggested by the results from the study of pollen stainability.

Based on the similarities in the morphology and the strongly annual growth habit, on the ease of making the crosses, on the regular chromosome behavior during meiosis and on the almost complete fertility in the F_1 plants, it is concluded by the author that these three cultivated varieties of O. glaberrima are closely akin to one another and there is no doubt that they belong to the same species. This conclusion will allow the author to use freely any of the three varieties as a representative of O. glaberrima in the studies of other interspecific hybrids whenever this species was involved.

(J) Crosses between O. sativa and O. glaberrima:-

Five varieties of O. sativa (Calrose, Colusa, Ziri, Impr. Blue Rose and Carolina Gold) and three varieties of O. glaberrima (Ekasa, Legheh and Kebleh) were involved in seven crosses between these two cultivated species in the studies. The glaberrima varieties were used as male parent in four of the seven crosses and as female parent in other three. Both ways of producing the hybrids proved successful.

The percentage of seed set from pollinated florets in making the crosses ranged from 36.8 to 63.4 with a mean of 46.6 % for the seven crosses included in the present studies. The consistent high percent seed set obtained from various varietal combinations

between these two species indicates the ease of making this type of cross.

In general morphology, the F_1 plants resembled the O. sativa parent in such characters as the roughness of leaves and the hairiness of the lemma and palea. However, the shape of the ligule was similar to that of the O. glaberrima parent except that it was longer in the F_1 plants. The stigma color of O. glaberrima varieties appeared to be dominant. An interesting feature shown in the F_1 plants was that the spikelets of all the hybrids were awned and the awn length was greater than both parents. This evidently was due to some kind of gene interaction. The empty spikelets of the sterile F_1 plants had a tendency to shatter. In growth habit, the F_1 hybrids were all strongly annual, a characteristic of the O. glaberrima parent.

From the cytological studies of diakinesis and MI, the frequency of rod-shaped bivalents per cell was found to range from 0.82 to 3.96 and the frequency of loosely held bivalents varied from 1.00 to 2.83 per cell at MI for the seven crosses.

The percentage of cells containing univalents at diakinesis and MI varied from 26.3 to 75.3 among the seven crosses. As shown in Table I, a very large number of cells having two univalents consistently occurred in all of the hybrids (Photo. 9 & 10). The frequency of cells containing four univalents was also relatively high in all of the F_1 plants (Photo. 11). Frequencies of cells with 6, 8-14 and 16-22 univalents varied in different crosses. However, they did occur commonly in all F_1 plants with two exceptions,

i.e., in hybrid No. 28 no cells with six univalents was found among the 544 PMCs examined and in hybrid No. 29 cells with 8-14 univalents were not observed among 419 PMCs. Representative photomicrographs showing cells containing 8, 12 and 20 univalents are presented (Photo. 12, 13 & 14). In certain crosses, such as hybrids No. 25 and No. 30, a very large number of cells were found to contain as many as 24 univalents indicating complete failure of pairing between the chromosome sets from the two species (Photo. 15 & 16).

In addition to the consistently high frequency of occurrence of univalents at diakinesis and MI, the loosely held condition of the bivalents was also prominent in this type of hybrid. As shown in Photo. 10 and Photo. 12, the stretched out configuration of bivalents at MI and the bivalents held only by a single chiasma at diakinesis all indicate the lack of complete homology between the two sets of chromosomes from O. sativa and O. glaberrima. However, as indicated previously, the frequency of loosely held bivalents per cell did not appear to be particularly high in these crosses. This was probably due to the fact that a great many cells contained univalents instead of bivalents and the frequency was calculated as number of loosely held bivalents per cell. In other words, if this had been computed on the basis of total bivalents it would be a higher value.

As indicated in Table II, the frequency of abnormal cells observed at AI ranged from 3.4 to 45.0 in the seven crosses. The abnormalities found at this stage included various numbers of laggards, unequal disjunction, bridge plus fragment and others.

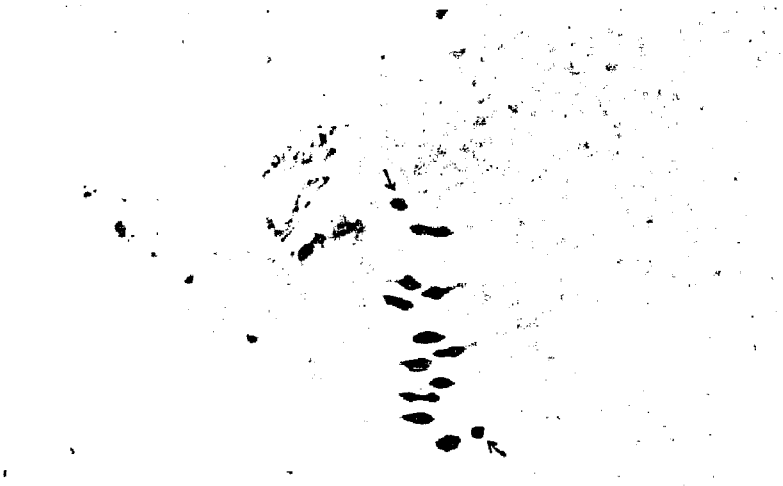

Photo. 9. Metaphase I in the F_1 plant of O. glaberrima (Ekasa) X O. sativa (Calrose) showing 11 bivalents and 2 univalents.

Photo. 10. Metaphase I in the F_1 plant of O. sativa (Ziri) X O. glaberrima (Ekasa) showing 11 bivalents and 2 univalents. Most of the bivalents are loosely held.

Photo. 11. Metaphase I in the F_1 plant of O. glaberrima (Ekasa) X O. sativa (Colusa) showing 10 bivalents and 4 univalents. One of the univalents has not moved to the equatorial plate.

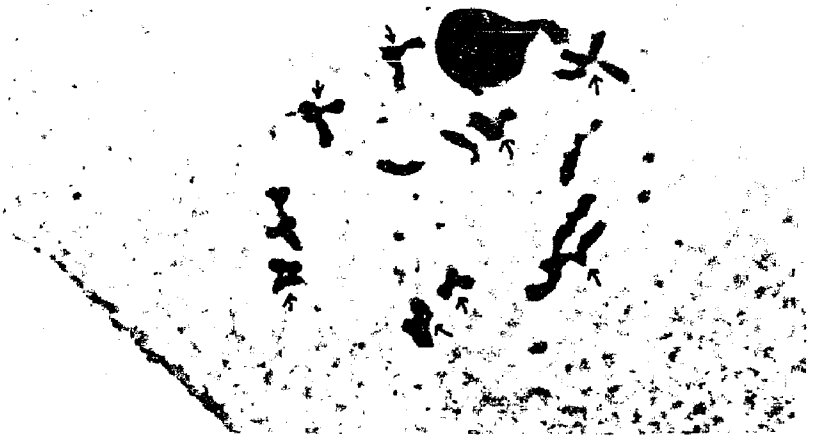

Photo. 12. Early diakinesis in the F_1 plant of O. sativa (Calrose) X O. glaberrima (Legheh) showing 8 bivalents and 8 univalents. Each of the bivalents are held by only a single chiasma. Arrows point to bivalents with single chiasma.

Photo. 13. Metaphase I in the F_1 plant of O. glaberrima (Ekasa) X O. sativa (Calrose) showing 6 bivalents and 12 univalents. Part of the bivalents are loosely held. Bivalents are indicated by arrows.

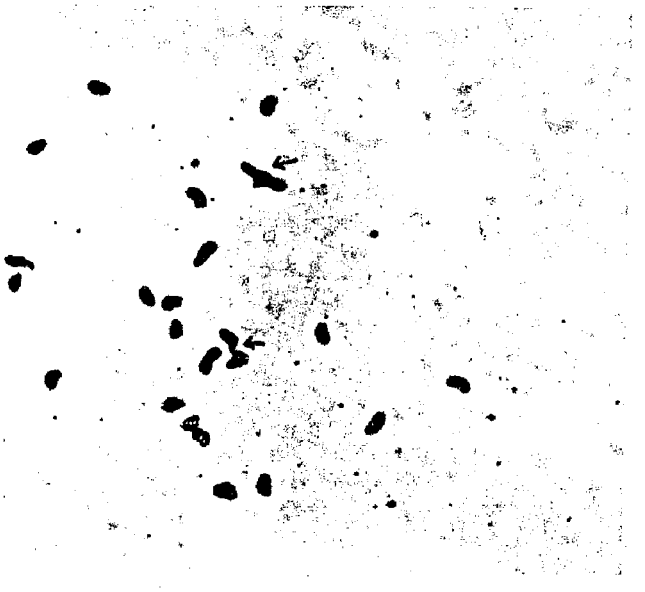

Photo. 14. Metaphase I in the F_1 plant of O. glaberrima (Ekasa) X O. sativa (Calrose) showing 2 bivalents and 20 univalents. Bivalents are indicated by arrows.

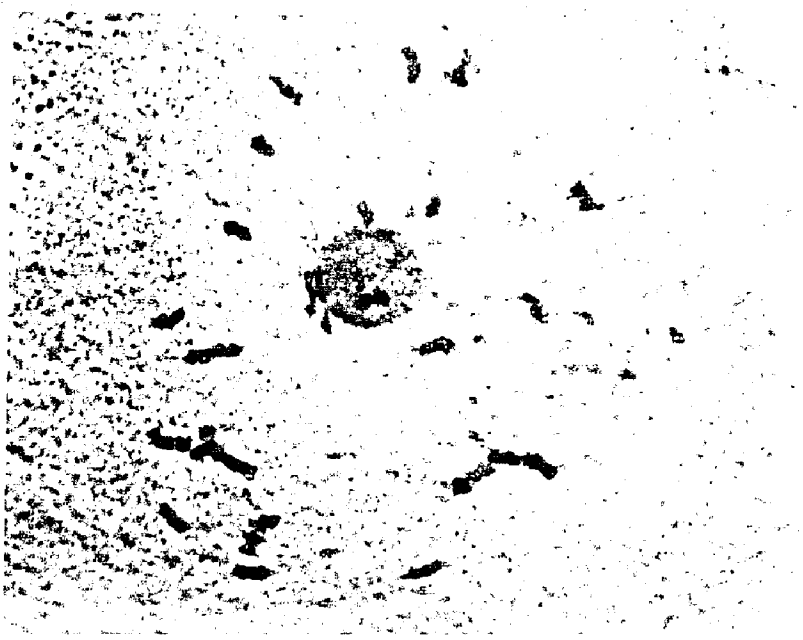

Photo. 15. Diakinesis in the F_1 plant of O. glaberrima (Ekasa) X O. sativa (Colusa) showing 24 univalents.

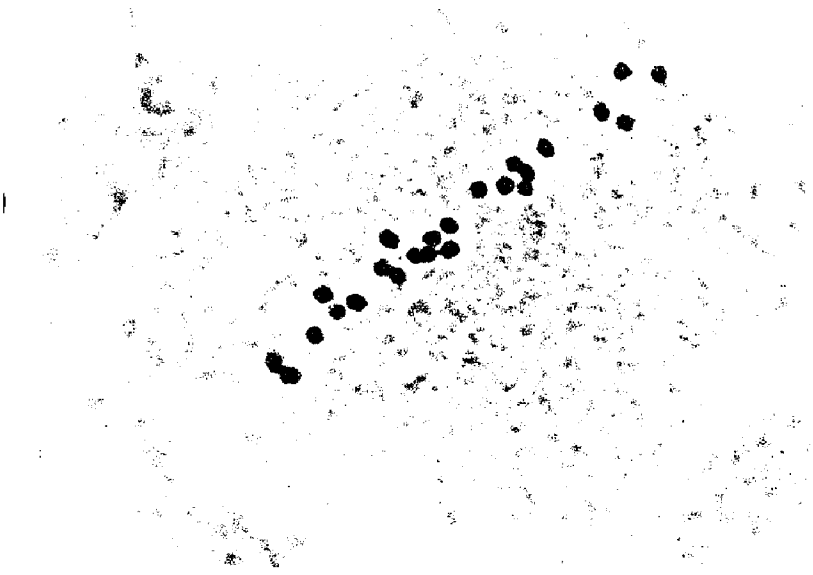

Photo. 16. Metaphase I in the F_1 plant of O. glaberrima (Ekasa) X O. sativa (Calrose) showing 24 univalents lined up on the equatorial plate.

The number of laggards found in each abnormal AI cell ranged from one to six. Some of them were lagging bivalents but most were lagging individual chromosomes which were undergoing equational division (Photo. 17 & 18). AI cells showing unequal disjunction were found to have 10 or 11 chromosomes at one pole and 14 or 13 chromosomes at the other pole. Cells containing bridge plus fragment were observed in four of the seven hybrids (Photo. 19). Abnormalities such as the occurrence of fragment without evidence of bridge and cells containing more than 24 chromatin bodies due to the division of some of the univalents present were also found.

As is also indicated in Table II, the percentage of cells with abnormalities at TI ranged from 0.0 to 1.3 among the seven hybrids studied. These abnormalities consisted of lagging chromosomes, traces of broken bridges and/or fragments. A photomicrograph representing a TI cell containing lagging chromosomes and fragments is shown (Photo. 20).

Other abnormalities were also noticed during the second division of meiosis. These abnormalities were the irregular arrangement of the two sets of chromosomes at MII and AII and the failure of cell wall formation between the cells of what would normally be a dyad at MII, AII and TII stages (Photo. 21, 22 & 23).

A minimum number of 300 microspore quartets was examined for each of the seven crosses. The percentage of abnormal quartets ranged from 0.0 to 77.7. Most of these abnormal quartets had the appearence of a large cell with four nuclei without a cell wall separating them (similar to what is shown in Photo. 23 at TII).

Even in the crosses which had 0.0 % abnormal quartets (hybrids No. 24, 25 and 26), most microspores had stopped development at the quartet stage with shrunken cell walls as evidence of the beginning of their deterioration.

The percentage of pollen stainable in aceto-carmine ranged from 0.0 to 5.9 in these hybrids. None of the F_1 plants set any seed, showing the complete sterility which was expected from the results on the study of pollen stainability.

Based on certain distinct morphological differences such as the glabrous condition of the plant parts and the short ligule in O. glaberrima, the lack of homology and possible structural differentiation of the chromosomes shown in the chromosome behavior at various stages during meiosis, the disturbed development of microspores and the complete sterility shown by pollen stainability and seed set, it is concluded by the author that the African cultivated form O. glaberrima is no doubt a distinct species from O. sativa. The cytogenetic relationship between these two spceies is much more distant than that found between O. sativa and other forms previously discussed.

(K) Cross between O. balunga and O. glaberrima:-

The only cross of this type included in the studies was made between the cultivated variety Ekasa of O. glaberrima and O. balunga. The latter was used as the male parent.

The percentage of pollinated florets which set seed in making the cross was 73.1. The cross proved easy to make and the F_1 seed

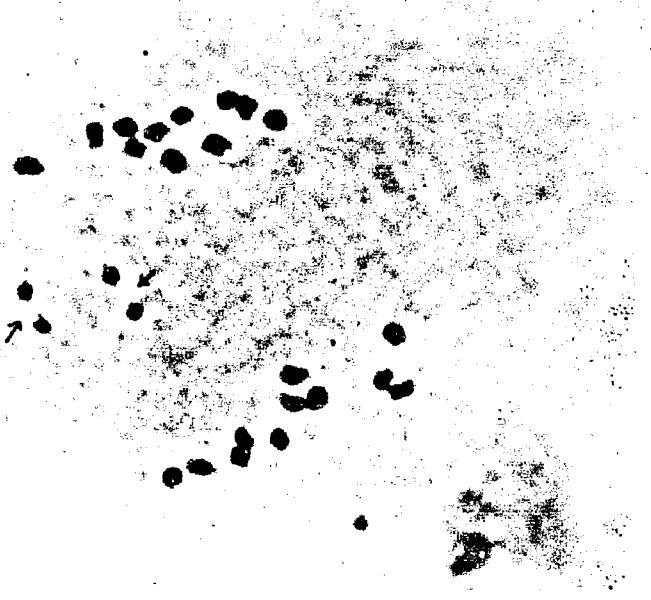

Photo. 17. Anaphase I in the F_1 plant of O. sativa (Colusa) X O. glaberrima (Legheh) showing two lagging chromosomes undergoing division characteristic of meiosis II. Apparently these two chromosomes were univalents at metaphase I.

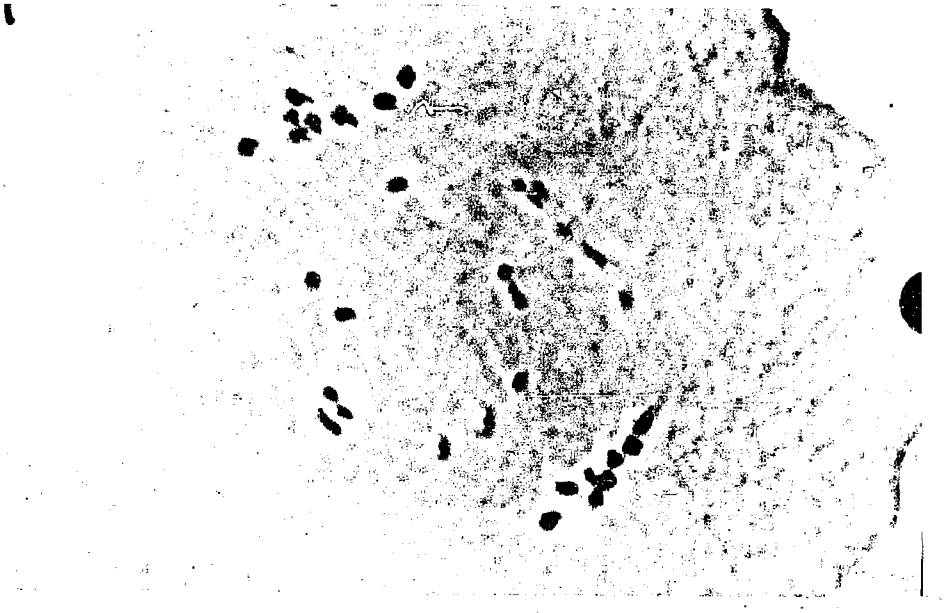

Photo. 18. Anaphase I in the F_1 plant of O. glaberrima (Ekasa) X O. sativa (Calrose) showing 8 lagging chromosomes undergoing division characteristic of meiosis II.

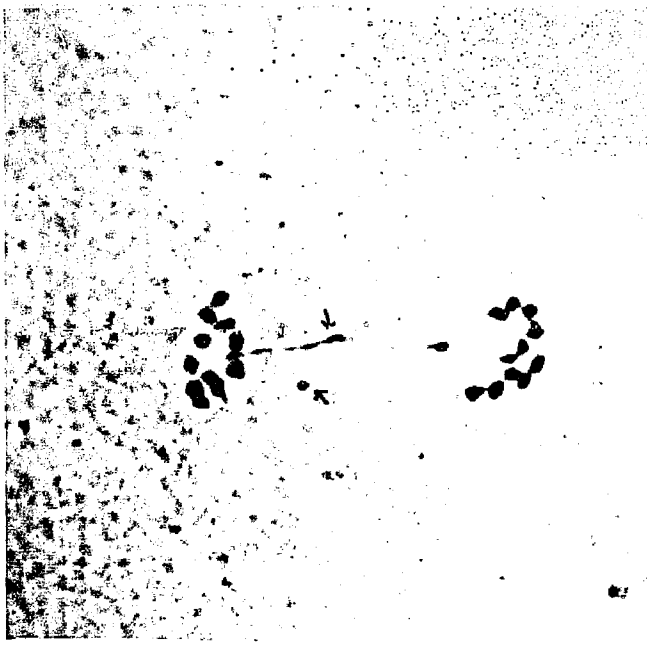

Photo. 19. Anaphase I in the F_1 plant of O. sativa (Impr.Blue Rose) X O. glaberrima (Legheh) showing bridge and fragment.

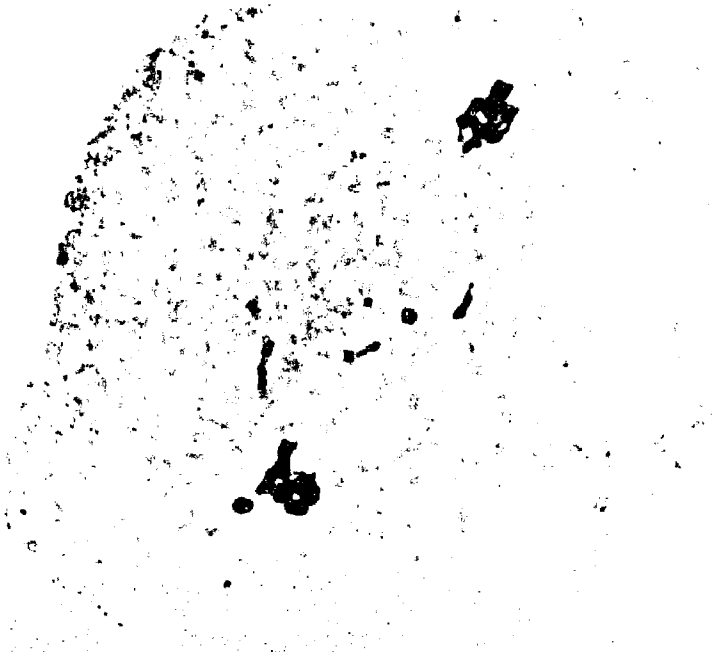

Photo. 20. Telophase I in the F_1 plant of O. sativa (Ziri) X O. glaberrima (Ekasa) showing lagging chromosomes and fragments.

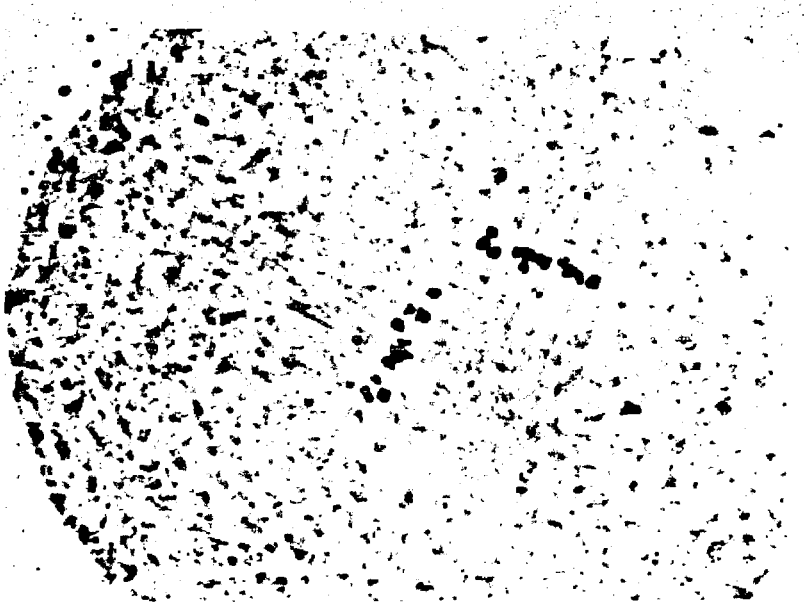

Photo. 21. Metaphase II in the F_1 plant of O. sativa (Colusa) X O. glaberrima (Legheh) showing absence of a cell wall between the two sets of chromosomes.

Photo. 22. Anaphase II in the F_1 plant of O. sativa (Colusa) X O. glaberrima (Legheh) showing absence of cell wall between the two nuclei and unequal disjunction in one nucleus.

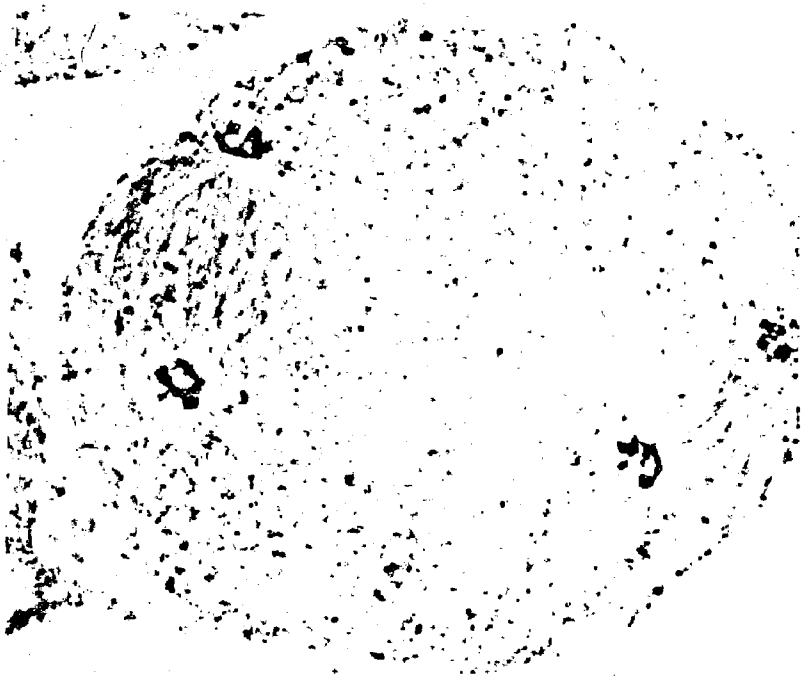

Photo. 23. Telophase II in the F_1 plant of O. sativa (Colusa) X O. glaberrima (Legheh) showing absence of cell wall between the nuclei.

Photo. 24. Late diakinesis in the F_1 plant of O. glaberrima (Ekasa) X O. balunga (O. perennis var. balunga) showing 11 bivalents and 2 univalents.

were well developed.

In general morphology, most characters of the F_1 plants such as shape and length of the ligule, shape of the panicle (semi-lax) and size of anthers were intermediate between the two parental forms. However, the hairiness of the leaves, the pigmentation of stems and the awn condition in the hybrid resembled O. balunga. In growth habit, the F_1 plants were semi-procumbent but had a tendency to root at the lower nodes of the stems as in the O. balunga parent. The plants were perennial and produced tillers continuously. The empty spikelets on the sterile F_1 plants shattered easily.

For the cytological studies at diakinesis and MI, 401 PMCs were examined for this F_1 hybrid. The frequencies of rod-shaped and loosely held bivalents per cell at MI were 1.90 and 1.52, respectively. These values are somewhat lower than the overall frequencies of these two types of chromosome pairing conditions obtained in the crosses between O. sativa and O. glaberrima. However, they are similar or higher to what was found in certain combinations in the previous type of cross.

The percentage of cells containing univalents at diakinesis and MI was 25.68, with large numbers of cells having two or four univalents each. However, no cell with more than four univalents was observed. Four photomicrographs showing cells with two or four univalents at diakinesis and MI are presented in Photographs No. 24, 25, 26 and 27. Again, the frequency of cells containing univalents observed in this cross is similar to that presented in

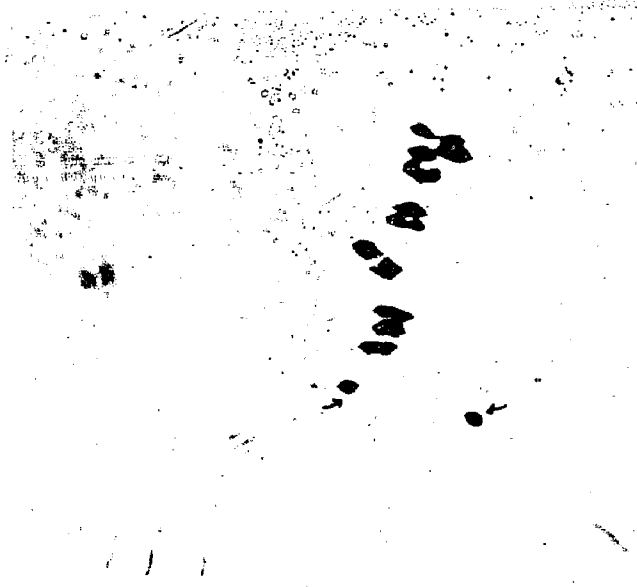

Photo. 25. Metaphase I in the F_1 plant of O. glaberrima (Ekasa) X O. balunga (O. perennis var. balunga) showing 11 bivalents and 2 univalents.

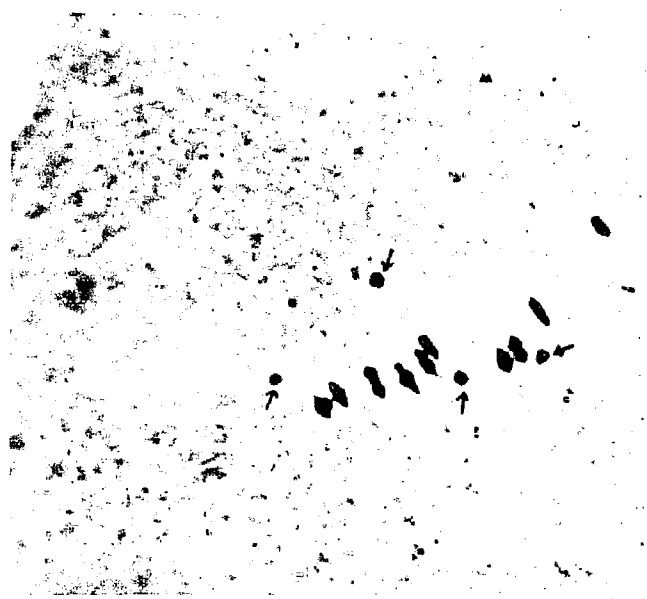

Photo. 26. Metaphase I in the F_1 plant of O. glaberrima (Ekasa) X O. balunga (O. perennis var. balunga) showing 10 bivalents and 4 univalents.

Photo. 27. Metaphase I in the F_1 plant of O. glaberrima (Ekasa) X O. balunga (O. perennis var. balunga) showing 10 bivalents and 4 univalents with one of the bivalents only loosely held. The double arrow points to the loosely held bivalent.

one of the combinations in crosses between O. sativa and O. glaberrima (hybrid No. 28).

As shown in Table II, 0.5 % of abnormal cells, containing 1-2 lagging chromosomes, were found among 396 PMCs examined at AI but all of the 350 PMCs studied at TI appeared to be normal. Comparing these results with what were obtained in crosses between O. sativa and O. glaberrima, the differences are probably due to combination effect. Since only one combination was studied for the O. glaberrima X O. balunga cross, it seems that not much importance could be attached to this inconsistency.

A very low percentage of stainable pollen, 4.5 %, and 0.0 % of seed set were obtained from the studies of the fertility of this cross. The complete sterility shown in this hybrid resembles that found consistently in the previous type of cross.

From results obtained in the studies of this hybrid and the crosses of O. sativa with O. balunga and O. glaberrima, the author concludes that O. glaberrima is also a distinct species from O. balunga. This conclusion is based on the extreme differences in the morphology and growth habit between O. glaberrima and O. balunga, the distant cytogenetic relationship between the two as shown in the results from meiosis and fertility studies of the hybrid which were similar to those obtained from the hybrids between O. sativa and O. glaberrima plus the fact that O. sativa and O. balunga proved very closely related to each other.

The ease of making the cross between these two species as shown in the high percentage of seed set on pollinated florets

seems to be a characteristic of O. glaberrima. A high percentage of seed set was always found whenever this species was involved in any cross.

(L) Crosses between O. glaberrima and O. breviligulata:-

Two cultivated varieties of O. glaberrima (Ekasa and Legheh) were hybridized with the wild African form O. breviligulata by using the latter as the pollen parent in both crosses.

The percentages of seed set from pollinated florets in making the crosses were 20.0 and 100.0 for O. glaberrima (Ekasa) X O. breviligulata (hybrid No. 32) and O. glaberrima (Legheh) X O. breviligulata (hybrid No. 33), respectively. The mean percentage was 28.0 because the value for the latter combination (100.0 %) was based on a smaller number of florets pollinated.

In appearence, the F_1 plants were very similar to O. breviligulata in such characters as the open panicle, the very long spikelets with long, rough awns and the hairy surface of lemma and palea. The hybrids also resembled O. breviligulata in respect to the early shattering of spikelets and the small plant type with weak straw.

Approximately 300 PMCs at diakinesis and MI were studied for each cross. The frequency of rod-shaped bivalents per cell were 4.78 and 4.33 and the frequency of loosely held bivalents were 0.79 and 0.40 for hybrids No. 32 and No. 33, respectively. These values are higher than those obtained in the homozygous varieties of O. glaberrima or in O. breviligulata itself but not

appreciably higher than what occurred in the F_1 hybrids between O. glaberrima varieties.

The percentages of cells with univalents at diakinesis and MI were 2.62 and 1.63 for the two hybrids, indicating a higher frequency of this abnormality than that found in the homozygous varieties of O. glaberrima. These values are also slightly higher than what was obtained in the O. breviligulata parent. However, they are comparable to the frequency of cells with univalents found in one of the varietal hybrid combinations within O. glaberrima (hybrid No. 23, 2.06 %). No cells containing more than two univalents were observed in these two hybrids between O. glaberrima and O. breviligulata.

As indicated in Table II, PMCs studied at AI and TI were all found to be normal.

The percentages of pollen stainable in aceto-carmine were 84.0 and 70.2 for the two crosses. The percentages of seed set on the F_1 plants of these hybrids were 52.3 and 54.6. These results indicate a moderate to high fertility of the F_1 hybrid between these cultivated and wild African forms.

Based on the results from cytological and fertility studies, it is concluded by the author that O. glaberrima and O. breviligulata are very closely related to each other. The cytogenetic relationship between the two is almost as close as that found between varieties within O. glaberrima. On the ground of this close cytogenetic relationship, the author agrees with the opinion of Chevalier (1932), which was also accepted by Chatterjee (1951),

that O. breviligulata was the putative ancestor of O. glaberrima. Despite the very close relationship between these two forms, however, the author also agrees with the classification made by Roschevicz (1931), Chevalier (1932) and Chatterjee (1948) that O. breviligulata should be recognized as a separate species from O. glaberrima on the basis of morphological differences, especially the complete glabrous condition of lemma and palea which characterizes O. glaberrima in contrast with the very pubescent condition of O. breviligulata.

(M) Crosses between O. glaberrima and O. stapfii:-

O. stapfii X O. glaberrima (Legheh) and O. glaberrima (Ekasa) X O. stapfii were the two crosses included in the study of this type of hybrid. No actual records were taken for the percentage of florets setting seed in making the crosses. However, the crosses proved easy to make and the F_1 seed were well developed.

Since the sample of O. stapfii used in the present researches resembled varieties of O. glaberrima closely, as described in the previous section, no special features were noticed in the morphology of the F_1 plants.

At MI of meiosis, the frequencies of rod-shaped bivalents per cell were 0.27 and 2.34 and the frequencies of loosely held bivalents were 0.29 and 0.12 per cell for the two crosses studied. These values are comparable and no higher than those obtained from O. stapfii itself and also no higher than what were found in crosses between varieties within O. glaberrima.

No cells containing univalents were found at diakinesis and MI among a total of more than 600 PMCs examined for the two crosses.

As shown in Table II, all PMCs examined at AI and TI were also found to be normal.

The percentages of pollen stainable in aceto-carmine were 99.8 and 94.2 for the F_1 plants of the crosses, indicating complete fertility. Seed set data was only taken for one of the crosses (hybrid No. 35). It was 83.9 %.

Based on the similarity in morphology of the two forms, the homology of chromosomes shown in their behavior during meiosis and the complete fertility observed in the F_1 plants, the author concludes that these two forms are very closely related to each other. The author is also inclined to agree with Chevalier (1932) in the opinion that O. stapfii should be considered as a variety of O. glaberrima on the grounds of the extremely close cytogenetic relationship obtained from the present studies and the fact that O. stapfii looked more like a cultivated form than a wild type, which was also pointed out by Chevalier (1932). However, only one collection of O. stapfii was available for the present study and the author does not feel that the results, consequently, are sufficiently extensive to permit a reliable decision on the question of whether O. stapfii should be recognized as a distinct species.

(N) Crosses between O. sativa and O. breviligulata:-

Three varieties of the cultivated rice O. sativa (Impr.Blue Rose, Colusa and Calrose) were hybridized with O. breviligulata

by using the latter as seed parent.

The percentage of pollinated florets setting seed ranged from 48.8 to 60.9 with a mean of 52.8 %. Thus, the crosses proved easy to make and the F_1 seed were developed normally.

In general morphology of the F_1 plants, the shape and length of ligule, the length of spikelets and the length of awns were intermediate between the two parents. The purple stigma color of O. breviligulata appeared to be dominant. The strong annual habit of this wild African form was also shown in the F_1 plants. The empty spikelets of the F_1 plant shattered but the shattering was not as pronounced as in O. breviligulata.

More than 400 PMCs of each cross were examined for the study of diakinesis and MI. The frequency of rod-shaped bivalents per cell ranged from 1.49 to 2.75 and the frequency of loosely held bivalents varied from 0.76 to 2.33 per cell among the three crosses. These values are similar and perhaps slightly lower than the overall frequencies of such conditions of the pairing of chromosomes in the crosses between O. sativa and O. glaberrima.

The percentage of cells with univalents ranged from 6.85 to 55.4 among the three crosses. Cells containing two, four and six univalents each were found in hybrid No. 36, which had the lowest frequency of cells with univalents. In hybrids No. 37 and No. 38, a large proportion of such abnormal cells were found to have two, four or 24 univalents each. The consistent occurrence of various numbers of univalents during diakinesis and MI also resembled what was observed in the F_1 plants of O. sativa X O. glaberrima and

indicate the lack of homology of the chromosomes from the two parental forms, O. sativa and O. breviligulata. Photomicrographs showing unpaired regions of chromosomes at pachytene stage and a cell containing eight bivalents and eight univalents at MI are presented in Photos. 28 and 29, respectively.

As shown in Table II, the percentage of abnormal cells at AI varied from 5.0 to 10.4 in the three crosses. The abnormalities included the occurrence of laggards, bridge plus fragment, unequal disjunction and others. Photomicrographs representing an AI cell containing unequal disjunction (10 + 14) and a late AI cell having a bridge plus fragment are shown in Photos. 30 and 31. The percentage of cells with abnormalities found at TI ranged from 1.6 to 2.1. Again, the nature of abnormalities found at AI and TI in this type of hybrid resemble those observed in the O. sativa X O. glaberrima F_1 plants and the frequencies of such abnormal cells found at AI and TI are also similar to what was obtained in certain crosses of the latter type hybrid.

A percentage of 1.07 for abnormal quartets were found in hybrid No. 37.

The percentage of stainable pollen in these crosses ranged from 0.4 to 51.9. However, it was noticed that pollen grains in the cross with the higher percentage of stainable pollen (hybrid No. 38) were not well developed and were only slightly stained in aceto-carmine. The percentage of seed set on the F_1 plants varied from 0.0 to 0.05, indicating virtually complete sterility in the F_1 of this type of hybrid.

Photo. 28. Pachytene in the F_1 plant of O. breviligulata X O. sativa (Impr.Blue Rose) showing unpaired regions in several of the bivalents.

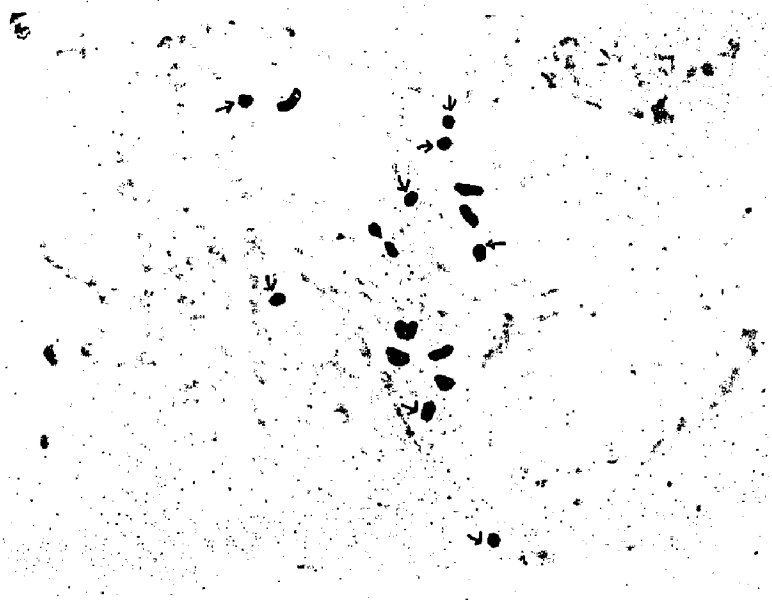

Photo. 29. Metaphase I in the F_1 plant of O. breviligulata X O. sativa (Impr.Blue Rose) showing 8 bivalents and 8 univalents.

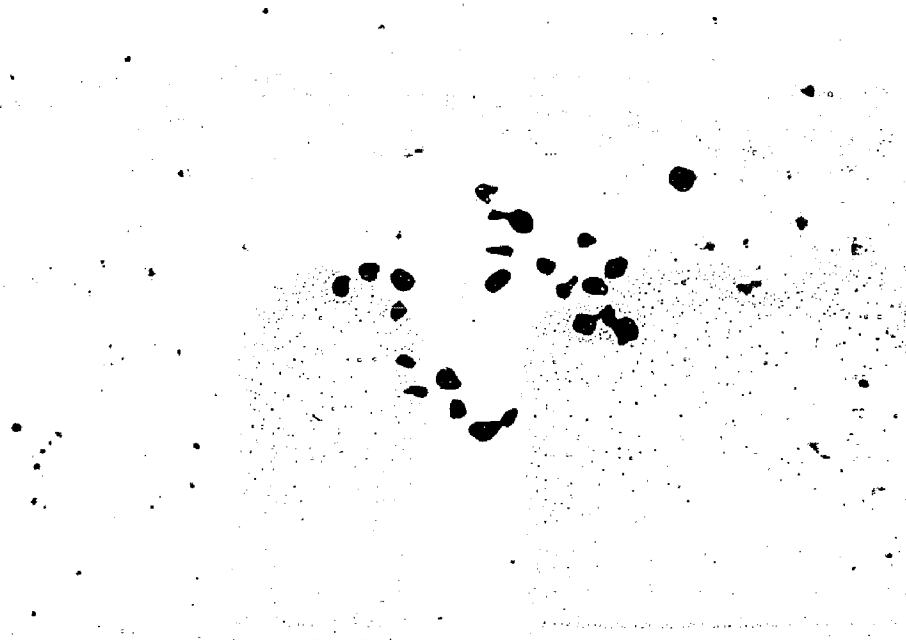

Photo. 30. Anaphase I in the F_1 plant of O. breviligulata X O. sativa (Impr.Blue Rose) showing unequal disjunction with 10 chromosomes moving to one pole and 14 moving to the other.

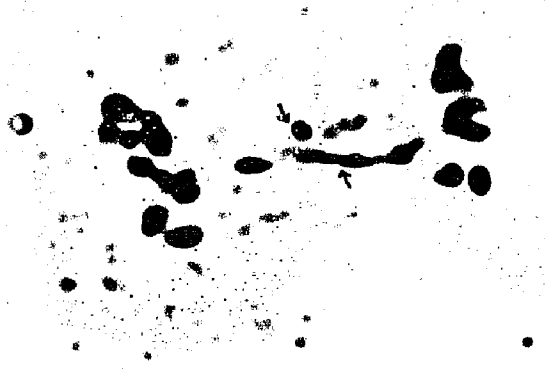

Photo. 31. Late anaphase I in the F_1 plant of O. breviligulata X O. sativa (Impr.Blue Rose) showing bridge and fragment.

It is concluded by the author, from the findings in the cytogenetic studies of the hybrids and the distinct morphological differences between the two parental forms, that O. breviligulata is certainly a separate species from O. sativa and the distant relationship between the two is similar to that found between O. glaberrima and O. sativa.

The similarity in the results obtained from cytological and fertility studies of this type of hybrids with those found in the crosses of O. sativa X O. glaberrima also confirms indirectly the conclusion made previously that O. breviligulata is very closely related to O. glaberrima.

(O) Crosses between O. sativa and O. stapfii:-

Two cultivated varieties of O. sativa (Fortuna and Ziri) were hybridized with O. stapfii, using the latter as the male parent. The percentages of pollinated florets setting seed when making the crosses were 35.2 and 46.4 for the two crosses (hybrids No. 39 and No. 40) with a mean of 42.1 %. F_1 seed were well developed.

In morphology of the F_1 plants, characters such as length and shape of the ligule and length of the spikelets were intermediate between the two parents but the hairiness of the leaves, and of the lemma and palea resembled O. stapfii. And, apparently due to some kind of gene interaction, the awn length in the F_1 hybrids exceeded that of both parental forms. As was true in all other crosses discussed, the purple color of stigma appeared to be dominant. No shattering of the empty spikelets was observed

in the F_1 plants.

Results from cytological studies of diakinesis and MI showed that the frequencies of rod-shaped bivalents per cell were 4.38 and 3.02 and the frequencies of loosely held bivalents were 1.21 and 3.33 per cell for the two crosses, respectively.

The percentage of cells containing univalents at diakinesis and MI were 29.30 and 40.68 for the two crosses. As indicated in Table I, a large proportion of such cells were found to have two or four univalents each in both hybrids. In addition to this kind of evidence showing the lack of homology between the chromosomes from the two parents, one cell with a quardrivalent (ring of 4) plus 10 bivalents was found in one of the crosses (hybrid No. 39), which indicates the heterozygous condition of a reciprocal translocation involving two non-homologous chromosomes.

Cells with abnormalities at AI were observed in both crosses. The percentages of such cells were 2.3 and 1.4 for hybrids No. 39 and No. 40, respectively. The abnormalities involved the occurrence of laggards as well as unequal disjunction. No abnormal cells were found at TI in hybrid No. 39. However, a low percentage (0.7) of cells with abnormalities was observed in hybrid No. 40. These were lagging chromosomes undergoing equational division.

The percentages of stainable pollen in these two crosses were 0.45 and 0.0, and no seed was set on the F_1 plants of either cross. This indicates complete sterility of the hybrids between O. sativa and O. stapfii.

Based on results from the cytogenetic studies of this type of hybrid, the author concludes that O. stapfii is a distinct species from O. sativa and the relationship between the two is similar to what was found between O. sativa and the other two African forms, O. glaberrima and O. breviligulata, that is, O. sativa and O. stapfii are distantly related species of the genus Oryza.

(P) Cross between O. sativa and O. officinalis:-

The only hybrid of this type included in the studies was the cross made between the cultivated variety, Ziri, of O. sativa and the wild form O. officinalis. The latter was employed as the male parent.

Several cultivated varieties of O. sativa in addition to Ziri were also used as seed parent in attempts to make this type of cross, but none of the combinations was successful except the one with Ziri. The overall percentage of pollinated florets which set seed was 10.9. (The percentage of seed set when crossed with Ziri was 21.7). However, the F_1 seed were poorly developed and only five seeds were germinable. Four of the F_1 seedlings died while small and only one of the five seeds produced an F_1 plant. Although the percentage of seed set from pollinated florets was not extremely low, this type of cross proved quite difficult to make due to the fact that pollin produced on the O. officinalis plants was scarce and a large portion of the pollen grains were aborted. The percentage of stainable pollen in O. officinalis

itself was 31.0 as indicated in Table II. The principal difficulty encountered, however, was death of 80 percent of the F_1 plants in the seedling stage.

In general morphology and growth habit, the F_1 plant resembled the O. officinalis parent very closely in almost every respect. However, it was very slow in development in the early stages and the new leaves were deficient in chlorophyll during the first few days after emergence from the next lower leaf sheath.

Although several young panicles were collected and fixed for the cytological studies of meiosis, PMC suitable for the research were very scanty. Of the 14 PMCs examined at diakinesis and MI, none of them was found to be normal. Various numbers of chromatin bodies ranged from 24 to 69 in different cells. Cells with 24 bodies evidently contained 12 bivalents and 12 univalents (Photo. 32).

At AI, only three PMCs were available for the study. These cells were found to be (1) a cell containing 12 and 11 chromosomes at the two poles and 13 chromosomes remaining between the poles undergoing division (Photo. 33), (2) a cell containing 12 chromosomes at each pole and 12 remaining in the middle and (3) a cell containing 36 chromosomes with some of them already undergoring equational division (Photo. 34).

Because of the abnormal numbers of chromosomes observed at diakinesis, MI and AI, the author suspected that some kind of polyploidy must have happened during the hybridization or the development of the hybrid embryo and an attempt was made to check

the somatic chromosome number of the F_1 plant from root tips. Results proved that this F_1 hybrid was a triploid with 2n = 36 chromosomes (Photo. 35). Since cytological material was not available for further study of meiosis, the constitution and origin of the 36 chromosomes in this triploid is still not clear.

Results from studies of pollen stainability and percent seed set indicate that this hybrid is completely sterile as expected from the cytological studies.

Based on the distinct morphological differences between the two parental forms, the difficulty encountered in making the cross, the triploid condition resulting from the hybridization, the disturbed chromosome behavior during meiosis and the complete sterility shown in the hybrid, the author feels there is no doubt that O. officinalis is a distinct species from O. sativa and the cytogenetic relationship between the two is quite distant.

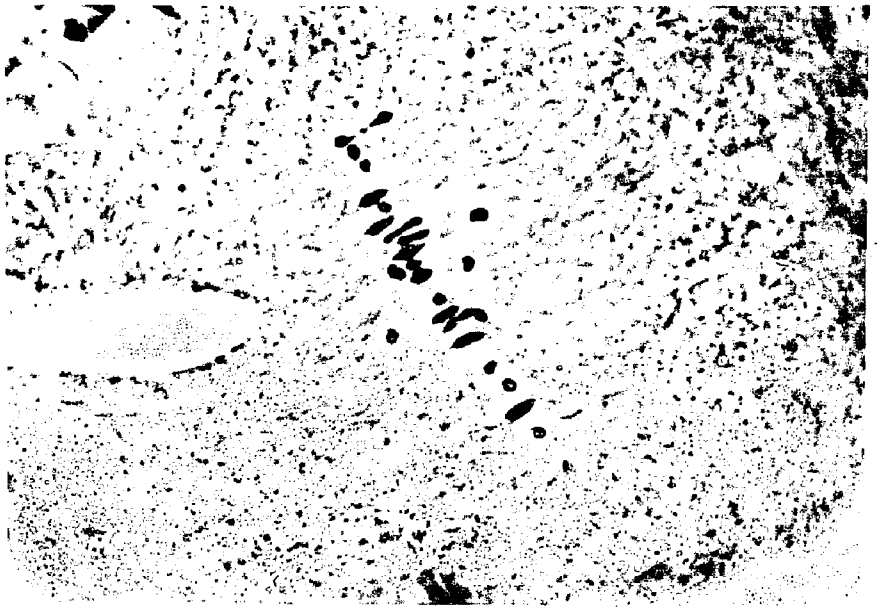

Photo. 32. Metaphase I in the F_1 plant of O. sativa (Ziri) X O. officinalis showing 12 bivalents and 12 univalents.

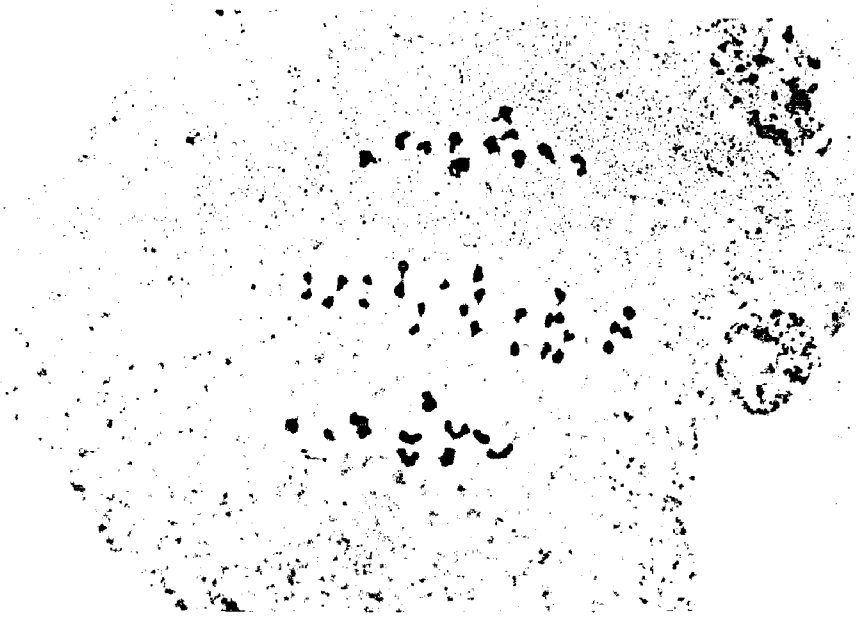

Photo. 33. Anaphase I in the F_1 plant of O. sativa (Ziri) X O. officinalis showing 12 chromosomes at one pole and 11 at the other and 13 chromosomes on the equatorial plate undergoing division characteristic of meiosis II.

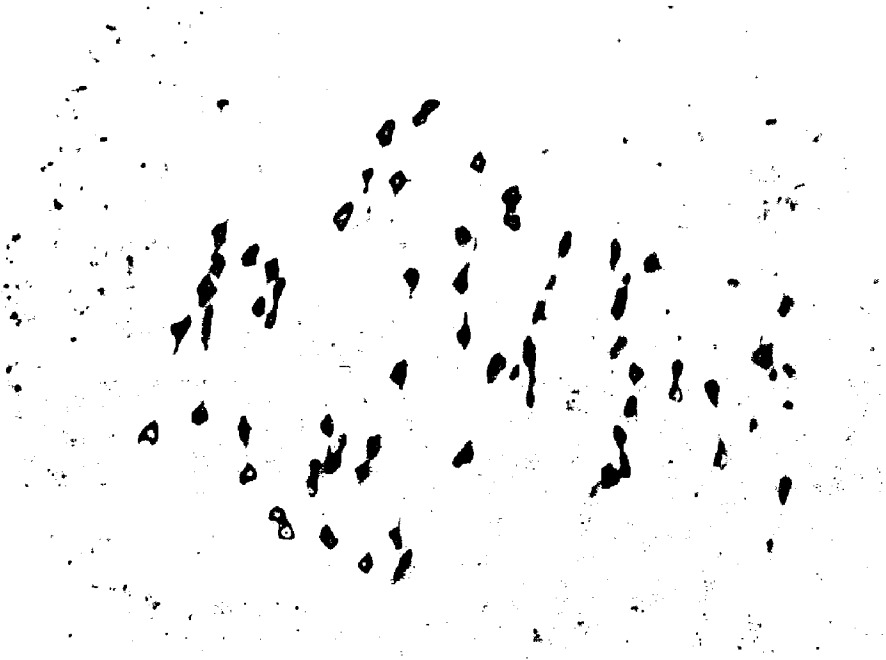

Photo. 34. Anaphase I in the F_1 plant of O. sativa (Ziri) X O. officinalis showing all the chromosomes undergoing division characteristic of meiosis II.

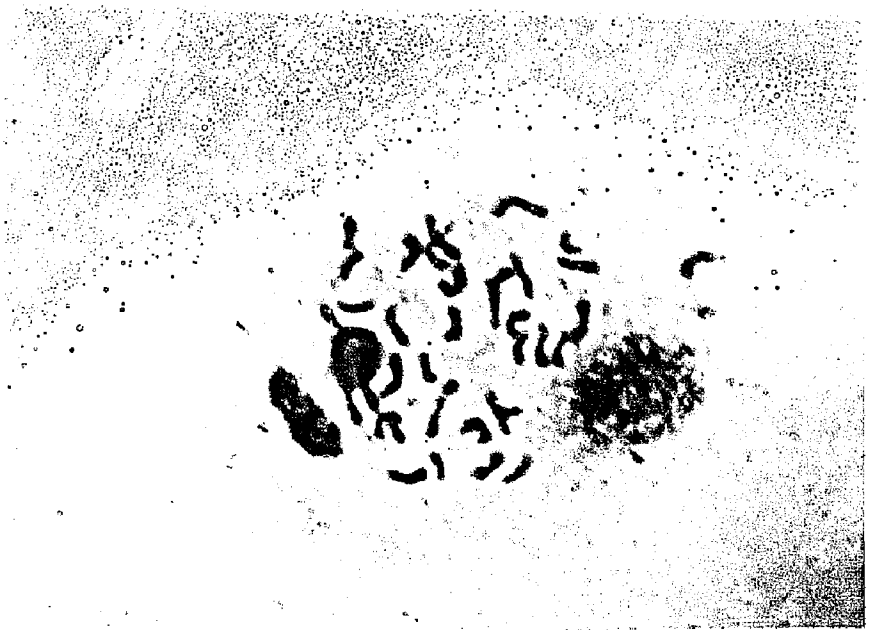

Photo. 35. Late prophase of mitosis in somatic cell of the F_1 plant of O. sativa (Ziri) X O. officinalis showing 36 chromosomes.

DISCUSSION

I. Recognition of Species in Oryza

As summarized and discussed by Dobzhansky (1941, 1951) and Stebbins (1950), after very extensive review of studies connected with the origin of species, the types of mechanisms which isolate species fall into two main catagories, namely, geographical or spatial isolation and reproductive or physiological isolation. The second catogory consists of (1) barriers between the parental species which include ecological, temporal and seasonal, mechanical isolations and the prevention of fertilization; (2) barriers in the hybrids which include hybrid inviability or weakness, failure of flowering in the hybrids, hybrid sterility (genic and chromosomal) and inviability and weakness of F_2 and later segregates.

Thus, based on these principal isolating mechanisms established in the origination of species, the general criteria commonly used as bases in recognition of species in plants consist of (1) the morphological characteristics of classical taxonomy, (2) geographical distribution, (3) crossability, (4) F_1 hybrid viability, (5) chromosome number, (6) chromosome behavior during meiosis in F_1, (7) hybrid fertility and (8) inviability and weakness or abnormal segregation in F_2 or later generations.

Earlier classifications of species were based almost entirely on differences in morphological characters, particularly traits of

the reproductive organs, and differences in geographical distribution. In recent years, data on the last six criteria of this list, which for convenience may be described as cytogenetic criteria, have been used to supplement the morphological characters and geographical distribution of classical taxonomy. Such information as whether two forms in question can be crossed readily, with difficulty or not at all; whether the forms have the same or different chromosome number; whether chromosome behavior during meiosis in the F_1 is regular or irregular; whether the hybrid is completely fertile, partially fertile or sterile; and whether weak or abnormal segregates occur in F_2 or later generations, is given weight along with morphological differences in deciding whether the forms should be recognized as being members of the same species or different species.

In some cases two spceies may differ in respect to all of the criteria listed in the previous paragraph. However, it is not necessary that two forms differ in all of these criteria for them to be placed in separate species. As applied in the genus Gossypium, a difference between two forms in any one of the cytogenetic criteria is considered sufficient to place the forms in separate species. Even in classification of Gossypium, however, due weight is given to morphological differences and geographical distribution in recognition of species.

As indicated in the 'Results' section, the author obtained cytogenetic evidence concerning relationships among forms in Oryza and attempted to use this information in evaluating the

principal earlier classifications of the genus, which were based largely on morphological characteristics. However, some of the cytogenetic criteria listed earlier did not appear to be applicable in the classification of Oryza. One such criterion was crossability of the various forms. Results obtained in the present studies and those reported in the literature indicate that the ease of crossing forms in Oryza is not a suitable criterion for distinguishing species because virtually all species in this genus can be hybridized readily, except in a few cases such as O. perennis var. barthii in which there are defects in sexual reproduction of the forms.

In the present studies only diploid forms of Oryza were included. For this reason, all forms contain the same chromosome number and this criterion, consequently, does not apply. Furthermore, the author did not follow the hybrid material beyond the F_1 generation and, as a result, the criterion involving segregation in F_2 or later generations could not be used.

Although fertility of the F_1 was used as a primary criterion in the studies, it was necessary to modify application of this evidence for recognizing species in Oryza. Normally all forms within a species produce completely fertile F_1 hybrids and the occurrence of any significant degree of sterility in F_1 is taken as evidence that the forms involved should be recognized as separate species. However, Oryza is unusual in that moderate to high degrees of sterility occur commonly in hybrids between some cultivated varieties of the same species O. sativa. As a consequence,

the occurrence in F_1 from crosses involving potentially different species of a moderate degree of sterility could not be used as evidence that these forms did represent separate species. Only when the one or more crosses between two forms were completely or almost completely sterile were the fertility data considered as providing evidence that the forms constituted separate species. If the degree of sterility in F_1 was similar to that found among intervarietal hybrids of O. sativa, the author did not consider this as evidence that the parental forms represented separate species.

Primary criteria used by the author as bases for distinguishing species of Oryza were (1) differences in morphology and in geographical distribution, (2) abnormal development or inviability of the F_1 hybrid, (3) abnormal chromosome behavior during meiosis in the F_1, and (4) complete sterility of the F_1 as discussed above.

Certain of the results can be cited to illustrate the nature of relationships found in the study and how the information obtained was applied. As indicated in the 'Results', the wild forms designated O. sativa var. fatua and O. sativa var. formosana did not differ from O. sativa in any of the cytogenetic criteria and had the same geographic distribution as this species. Since these two wild forms differed from O. sativa only in minor morphological characters, they were considered to be botanical varieties of O. sativa rather than distinct species.

The case of O. sativa var. formosana was somewhat uncertain. Because of its perennial nature and very close cytogenetic relation-

ship, this form might also be considered a botanical variety of O. balunga. The decision to place it in O. sativa was based on the closer morphological similarity which it showed to that species.

Although the cytogenetic relationship between O. sativa and the wild perennial form found in India and designated O. perennis var. balunga by Sampath & Govindaswami (1958) and O. balunga in the present studies was sufficiently close to justify placing these forms in the same species and the geographic distribution is similar, the author feels that the distinct differences shown in morphology and growth habit of these forms are sufficient to warrant a separate species' status for the wild perennial type. Thus, this example illustrates the conventional separation of species on the basis of prominent differences in morphology and growth habit even though the cytogenetic data indicate an extremely close relationship between the two forms concerned. Recognition of separate species' status for O. glaberrima and O. breviligulata is based on the same type of evidence.

The relationship between O. sativa and O. perennis is somewhat different from the above. Here, in addition to the distinct differences in morphology and growth habit, F_1 hybrids of all combinations involving these two forms were completely or almost completely sterile. Although the essentially regular chromosome behavior during meiosis in these hybrids indicates a close relationship between the two forms, it is felt that the high sterility

found in all hybrid combinations indicates a reproductive barrier between these species providing evidence that they, O. sativa and O. perennis, not only should be recognized as separate species but are less closely related than are O. sativa and O. balunga.

The relationship between O. sativa and O. glaberrima provides an example of a still greater differentiation of species in Oryza. These two forms differ sufficiently in several criteria to justify recognition as separate species. They differ not only in morphological characteristics and native habitats, but all hybrid combinations were completely sterile and, unlike the previous examples cited, chromosome behavior during meiosis in the hybrid was irregular. The author interprets these results as indicating that O. sativa and O. glaberrima are not closely related species and that the relationship is more distant than that between O. sativa and O. perennis. O. sativa and O. breviligulata represent an additional example of a somewhat distant relationship that is comparable to that between O. sativa and O. glaberrima.

Data from studies of the hybrid between O. sativa and O. officinalis, though admittedly limited, agree with those reported by earlier workers and indicate a more distant relationship of O. officinalis to O. sativa than was found between O. sativa and any other diploid species included in the present studies. This more distant relationship is shown primarily by inviability of most F_1 plants in the seedling stage, absence of pairing between chromosomes of O. sativa and O. officinalis and major differences in morphology.

The recognition by the author of the wild perennial floating rice of South East Asia as a separate species from O. perennis requires special consideration, as indicated previously in 'Results'. The existence of this form has only been known since 1951. Rice workers in India have classified it as being a form of O. perennis and it was designated as O. perennis var. balunga by Sampath and Govindaswami (1958). The classification of this wild Asiatic form as a variety of O. perennis was based on the presence of a long ligule and its perennial nature. Actually this form differs appreciably from the American and African forms of O. perennis in appearence and there is considerable doubt that it should be placed in the same species with O. perennis because of differences in morphology alone.

In addition, the writer obtained indirect evidence from studies of hybrids between O. sativa and the perennial Asiatic form and between O. sativa and O. perennis which also indicated that the perennial Asiatic form should be considered a separate species from O. perennis. As indicated earlier, an extremely close cytogenetic relationship was found between O. sativa and the perennial Asiatic form. In all respects, this cytogenetic relationship was as close as that between cultivated varieties of O. sativa. On the other hand, although the cytogenetic relationship between O. sativa and O. perennis was reasonably close, the occurrence of almost complete sterility in all crosses involving these two species indicates a more distant relationship between O. sativa and O. perennis. Because of the appreciable difference in mor-

phology between O. perennis and the perennial Asiatic form and the indirect cytogenetic evidence described above, the author feels that the perennial Asiatic form should be treated as a separate species instead of a botanical variety of O. perennis. However, cytogenetic evidence of a direct nature should be obtained for these two forms before an entirely reliable conclusion can be drawn. Material to provide this evidence is now being grown.

II. Genomes in Oryza

The subject of genomes in Oryza apparently has been discussed previously only by Morinaga (1938, 1943, 1956) and Morinaga and Kuriyama (1957). These workers studied chromosome pairing at MI in hybrids of O. sativa with seven other diploid forms, designated O. glaberrima, O. breviligulata, O. perennis, O. cubensis (O. perennis var. cubensis in the writer's classification), O. sativa var. fatua, O. sativa var. spontanea and O. formosana (O. sativa var. formosana in the writer's classification) and reported 12 bivalents as occurring regularly. From these results they concluded that all of these diploid forms have the same genome, which was designated as genome A by Morinaga in 1943. Based on absence of pairing in F_1 of hybrids between O. sativa and two tetraploid species, O. minuta and O. latifolia, Morinaga concluded that these two tetraploid species do not contain genome A. Since he found in the hybrid O. minuta X O. latifolia 12 bivalents and 24 univalents,

he concluded that these two tetraploid species contain one genome in common but differ in respect to the second genome. From these results the genomes of O. minuta were designated B and C and those of O. latifolia were designated C and D.

The cytogenetic evidence obtained in the present studies can also be used for analyzing the genome constitution among the 10 diploid forms included in this research. The system followed for designating genome constitution of the forms studied in this dissertation is based on the apparent degree of cytogenetic relationship between the forms in question. The cytogenetic evidence included in designating genomes involved chromosome pairing during meiosis in F_1 and degree of sterility of F_1. If chromosome behavior during meiosis in the F_1 was found to be "normal" and the hybrid showed no higher degree of sterility than found in intervarietal hybrids of O. sativa, the two parental forms were concluded to have the same genome, which was assigned a letter designation. (The expression "normal" in regard to chromosome behavior in F_1 indicates that irregularities such as univalents at diakinesis and MI were no more frequent than commonly found among intervarietal hybrids of O. sativa.)

If the chromosome behavior during meiosis in the F_1 was essentially normal but the hybrid was completely or almost completely sterile, the two parental forms involved in the cross were considered to contain the same basic genome but with small differences of a genetic or chromosome structural nature. In such cases, the genomes in the two forms concerned were designated with

the same letter but were assigned different subscript numbers.

If significant irregularities in the chromosome behavior were found during meiosis in the F_1 and the hybrid was completely or almost completely sterile, the two parental forms were considered to have different genome constitutions. In these cases, the genomes of the species involved were assigned different letters to indicate their cytogenetic differentiation.

As reported in 'Results', in crosses of O. sativa with the wild forms O. sativa var. fatua, O. sativa var. formosana and O. balunga chromosome behavior in meiosis was normal and the hybrids showed a high degree of fertility. From these results, it was concluded that these four forms contain the same genome. Since the letter A has already been used by Morinaga for the genome in O. sativa, the author adopts it as the genome designation for these forms.

In F_1 of hybrids between O. sativa and the two forms of O. perennis, var. cubensis and var. barthii, and between O. sativa var. formosana and O. perennis var. cubensis, chromosome behavior during meiosis was normal but the hybrids were almost completely sterile. Consequently, it was concluded that the species O. perennis contains genome A but that it is differentiated sufficiently from the genome of O. sativa to warrant separate subscript numbers. The author suggests that the genome of O. sativa and the other closely related forms referred to in the previous paragraph be designated A_1 while the genome of O. perennis var. cubensis and O. perennis var. barthii be designated A_2.

In F_1 of several hybrids between varieties of O. sativa and O. glaberrima, chromosome behavior in meiosis was definitely irregular and all hybrids were completely sterile. These results indicate that O. sativa and O. glaberrima contain sufficiently different genomes to justify different letter designations. Since the letters B,C and D have already been used by Morinaga to represent genomes in the tetraploid species, O. minuta and O. latifolia, the author adopts the letter E to designate the genome of O. glaberrima. However, it would be more logical if the genome designation in the tetraploid species could be assigned after genome analysis of the various diploid forms of Oryza has been completed.

As also indicated in 'Results', two other African diploid species, O. breviligulata and O. stapfii, were found to be very close to O. glaberrima in their cytogenetic relationships, a relationship comparable to that found between O. sativa and its botanical varieties and O. balunga. Hence, it is concluded that O. breviligulata and O. stapfii also contain genome E. Genome E appears to be more closely related to genome A than are the genomes B, C and D of the tetraploid species O. minuta and O. latifolia.

A very distant cytogenetic relationship was found between O. sativa and O. officinalis. This suggests that O. officinalis contains still another genome distinct from genomes A and E. However, since it seems probable from morphological similarities that O. officinalis contains one of the two genomes B and C of O. minuta, the author has not adopted a genome designation for

O. officinalis. The proper genome designation for O. officinalis will have to await cytogenetic studies in hybrids of this species with the tetraploid forms O. minuta and O. latifolia.

For convenience of the reader, information concerning genome constitution of the 10 diploid forms investigated in the present research is presented in Table III.

Table III. Proposed genome constitution of 10 forms of Oryza

Species	Genome constitution
O. sativa	A_1A_1
O. sativa var. fatua	A_1A_1
O. sativa var. formosana	A_1A_1
O. balunga	A_1A_1
O. perennis var. cubensis	A_2A_2
O. perennis var. barthii	A_2A_2
O. glaberrima	E E
O. breviligulata	E E
O. stapfii	E E
O. officinalis	*

* Not genome A or E.

As cited previously, Morinaga (1956) and Morinaga & Kuriyama (1957) reported that in F_1 hybrids between O. sativa and O. glaberrima and between O. sativa and O. breviligulata meiosis was regular

with the formation of 12 bivalents at MI and on the basis of this evidence the authors concluded that O. glaberrima and O. breviligulata contain the same genome as O. sativa. The results obtained by the author in hybrids of O. sativa with these two African species were contradictory to those reported by Morinaga and Morinaga & Kuriyama. As shown in Table I and II, and in photographs No. 9-23 and No. 28-31, considerable irregularity in chromosome behavior during meiosis in these hybrids was found. The author is unable to explain the contradiction in these results. However, the report of complete sterility in all crosses between O. sativa and O. glaberrima by Morinaga and Kuriyama agrees with the findings in the present research.

III. Origin of the Cultivated Species of Rice, O. sativa and O. glaberrima

Two principal proposals concerning the origin of the world wide cultivated rice O. sativa have been put forth and supported by various workers.

(1) The first of these theories to be put forth is that O. sativa originated from the highly variable closely related annual wild type designated O. sativa var. fatua or O. sativa f. spontanea. It is assumed in this theory that the origin occurred in Southeast Asia, probably India. The opinion that O. sativa was derived from closely related wild forms in Southeast Asia is generally

credited to Watt (1891). Watt and several other earlier workers expressed the opinion that most cultivated varieties of O. sativa were derived from one wild form but that some varieties had originated from other species. As mentioned in the 'Review of Literature', however, it has been established from cytogenetic evidence, such as chromosome number, that these other wild species could not have been progenitors of O. sativa.

Ever since the classification of the genus Oryza by Roschevicz (1931), the variable wild form proposed as the progenitor of O. sativa in this theory has generally been considered to represent a botanical variety of the species O. sativa, although such workers as Chevalier (1932) and Chatterjee (1948) expressed the opinion that this form should be recognized as a separate species. As brought out in the 'Results' and an earlier topic of 'Discussion' in this dissertation, the writer agrees with the opinion that this wild form should be considered a botanical variety of O. sativa and that the proper name is O. sativa var. fatua.

The theory that O. sativa was derived from O. sativa var. fatua has been widely accepted and until 1951 was essentially the only hypothesis that was generally accepted. Evidence upon which this theory was based includes: (i) there is a very close morphological similarity between O. sativa and O. sativa var. fatua; (ii) O. sativa var. fatua occurs commonly and is apparently endemic in the region of greatest genetic diversity, South East Asia, found in O. sativa and assumed, consequently, to be

the place of origin of O. sativa; (iii) O. sativa var. fatua has the same chromosome number as O. sativa, hybridizes readily with it and the hybrids are partially to completely fertile.

Without a doubt O. sativa var. fatua shows the closest morphological resemblance to O. sativa of any wild forms. In fact, this close resemblance has led most taxonomists to treat it as a variety of O. sativa. The greatest degree of genetic diversity in O. sativa occurs in Southeast Asia and it is generally assumed that O. sativa originated there. Since O. sativa var. fatua is associated with the growing of O. sativa in that area and actually constitutes a weed in cultivated field, it is assumed that this common habitat for the two forms provides further evidence that O. sativa var. fatua is the progenitor of O. sativa. Cytogenetic evidence, including that found in the present studies, confirms the conclusion that O. sativa var. fatua is very closely related to O. sativa and could have been the progenitor of this cultivated species.

(2) The second theory proposed more recently is that O. sativa was derived by human selection in Southeast Asia from the wild species O. perennis rather than from O. sativa var. fatua. This hypothesis was put forth by Sampath and Rao (1951). The wild form referred to by Sampath and Rao as the probable progenitor of O. sativa is a perennial floating type Asiatic form which they classified as O. perennis and was later designated O. perennis var. balunga by Sampath and Govindaswami (1958). For reasons presented earlier in this dissertation, the writer

concludes that this wild Asiatic form represents a separate species from O. perennis for which the name O. balunga has been adopted.

This new proposal that O. sativa was derived from a wild Asiatic form considered by Sampath and Rao to be O. perennis was based on evidence that (i) O. perennis has the widest distribution of all wild species of Oryza---Asia, America and Africa---and is found commonly in India and Ceylon; (ii) O. perennis has 2n = 24 chromosomes also characteristic of O. sativa, has been hybridized with O. sativa and the hybrids were fertile; (iii) the grains of O. perennis are long and slender and the fact that they would be attractive to man is shown by evidence that it is being harvested today in the State of Orissa (India); (iv) because of the extreme degree of genetic variation in O. sativa var. fatua, Sampath and Rao concluded that "such a complex and artificial group as spontanea paddies are not likely to be a species ancestral to O. sativa."

It appears from the cytogenetic evidence obtained in the present studies that the second of these theories requires some modification, at least in respect to manner in which the theory is stated. As indicated previously, the writer found that hybrids between O. sativa and both the American and African forms of O. perennis were almost completely sterile, a condition contradictory to the claim by Sampath and Rao that these hybrids are fertile. It is obvious from these results that the wild progenitor proposed in the second theory should be restricted exclusively to the peren-

nisl floating type form of Oryza that is endemic to Southeast Asia, a form which the writer prefers to consider a separate species, O. balunga, rather than a variety of O. perennis.

It is apparent that any proposal concerning the origin of O. sativa should take into account the following facts: (i) There is no evidence of any cytogenetic differentiation between O. sativa and either of the two wild forms, O. sativa var. fatua and O. balunga, indicating an extremely close relationship among these types. If either one of these two wild forms is assumed to be the progenitor of O. sativa, the close relationship between O. sativa and the other wild form must be accounted for. (ii) Although O. balunga and O. sativa var. fatua are both designated as wild types, only O. balunga of these two forms is unquestionably a truly wild type that does not show any evidence of influence by man. Many, if not most, existing forms of O. sativa var. fatua show so many characteristics of cultivated rice that would be of no advantage in nature that it is highly questionable whether this form can be considered as truly wild. In fact, O. sativa var. fatua exists primarily through association with the cultivation of rice. (iii) Numerous reports from Southeast Asia indicate that O. sativa var. fatua is a highly variable form, showing genetic diversity in many traits. This is in contrast to the relatively low degree of genetic variation reported for O. balunga. It is difficult if not impossible to account for the wide genetic variation in a self fertilized plant like O. sativa var. fatua without assuming that man has had some influence on this form. It is improbable that the genetic variation found

in fatua could have arisen under natural conditions.

Based primarily on cytogenetic relationships between O. sativa and the wild forms included in the present research, the author feels that there are two probable paths through which O. sativa may have evolved. The first of these is that O. sativa was derived directly from O. balunga through domestication by man and that O. sativa var. fatua originated from natural hybrids between O. sativa and O. balunga and between O. sativa and O. sativa var. fatua itself after the latter type had become established. In view of the facts cited in the previous paragraph, this theory is entirely logical. It will account for the extremely close cytogenetic relationship between O. sativa and O. balunga as well as the highly variable condition of the forms which are classified as O. sativa var. fatua today. The observation by Sampath and Rao (1951) that the grain of O. balunga is sufficiently attractive to man that it is some time harvested in certain areas of India makes the proposition that O. sativa was derived from O. balunga even more acceptable.

A second possibility is that O. sativa was derived from O. balunga but only indirectly, with such forms as O. sativa var. formosana and var. fatua serving as intermediate stages in the domestication procedure. In other words, var. formosana and var. fatua may have been derived from O. balunga as the first steps in domestication and these forms rather than O. balunga may have been the immediate progenitors of O. sativa. This suggestion is based on the fact that O. sativa var. formosana

and certain types of O. sativa var. fatua are similar in morphology to O. sativa but are intermediate between O. sativa and O. balunga in many respects, including growth habit.

All of the critical evidence bearing on this subject indicates that cultivated rice belonging to O. sativa was derived directly or indirectly from the distinctly wild closely related species O. balunga. It is probable that the earliest types of domesticated rice derived from O. balunga resembled var. formosana, which still possesses the perennial habit and the ability to float in deep water but is less procumbent and produces more grain than O. balunga. It is also probable that some of the early types of cultivated rice would now be classified as O. sativa var. fatua if they are still in existence. The only distinction between var. formosana and var. fatua is the perennial habit of the former contrast to the annual habit of the latter form.

In making the above suggestions, it is assumed by the writer that in the domestication of rice the plant gradually lost its perennial habit and became an annual through the selection pressure placed by man on seed formation, that erect types characteristic of current varieties of O. sativa were obtained step by step from the prostrate O. balunga through selection of forms better suited to cultivation and that at the same time the shattering characteristic of O. balunga was gradually replaced by forms with less tendency to shatter.

It is considered probable, however, by the writer that most forms of O. sativa var. fatua in existence today arose from

natural hybridization between cultivated rice and O. balunga and/or between cultivated rice and still existing primitive forms of fatua. The evidence that many and perhaps most forms of fatua now in existence arose by hybridization involving modern types of cultivated rice is highly convincing. For example, the strain of fatua included in the present studies does not show primitive characteristics that would be expected in a wild progenitor of cultivated rice. If it is assumed that the only domestication processes were those involving the change from O. sativa var. fatua to O. sativa, it is also necessary to assume that forms characteristic of O. sativa var. fatua arose from O. balunga in nature. This does not appear to be probable.

Thus, it appears most probable to the writer that the early domesticated forms of rice were types similar to O. sativa var. formosana, that these primitive domesticated forms were derived from O. balunga and that they served as the immediate progenitors of our cultivated rice. This conclusion, however, does not exclude the possibility that certain of the early domesticated types were annual and would be classified as O. sativa var. fatua. These conclusions and other lines of evidence leave little doubt that the cultivated species O. sativa originated in Southeast Asia.

Chevalier and Roehrich (1914) and Chevalier (1932) concluded that the cultivated form O. glaberrima found only in tropical West Africa was probably derived from the related wild African species O. breviligulata. Several other investigators, notably Roschevicz (1931) and Porteres (1956), have accepted this proposal. However,

Ramiah and Ghose (1951) questioned whether O. glaberrima should be considered as a separate species from O. sativa. Sampath and Rao (1951) suggested that both O. sativa and O. glaberrima were probably derived from O. perennis.

Cytogenetic evidence obtained in the present studies agree strongly with the conclusion that O. glaberrima was derived from O. breviligulata and should be considered a separate species from O. sativa. As indicated earlier, a somewhat distant cytogenetic relationship between O. sativa and O. glaberrima is shown by irregular chromosome behavior during meiosis in the F_1 and complete sterility of the hybrid. On the other hand, an extremely close relationship, comparable to that found between O. sativa and O. balunga, was found between O. glaberrima and O. breviligulata. Furthermore, the writer has indirect evidence that the relationship between O. glaberrima and O. perennis is relatively distant. This is based on the close relationship found between O. sativa and O. perennis plus the distant relationship between O. sativa and O. glaberrima. It is on these grounds that the writer agrees with the conclusion by Chevalier (1932) that O. glaberrima was derived from O. breviligulata, hence has a different origin from that of O. sativa.

As to the place of origin, there is no doubt that O. glaberrima is indigenous to tropical West Africa.

SUMMARY

The cytogenetic relationships between the common cultivated rice, O. sativa, and nine other diploid forms of Oryza were studied. The nine forms included were O. sativa var. fatua, O. sativa var. formosana, O. balunga (O. perennis var. balunga), O. perennis var. cubensis, O. perennis var. barthii, O. glaberrima, O. breviligulata, O. stapfii and O. officinalis. Crosses were made between O. sativa and all of these forms as well as between some forms among the nine. A total of 41 hybrids representing different species combinations were included in the research.

Studies were made on the morphological characteristics of the parental forms and their F_1 generation hybrids, on the crossability of the species, on the chromosome behavior during meiosis in F_1 plants and on the relative fertility of the F_1 hybrids (based on both the pollen stainability and percent seed set).

Cytogenetic studies of the hybrids of O. sativa with O. sativa var. fatua, O. sativa var. formosana and O. balunga indicated that these three wild Asiatic forms are very closely related to O. sativa. Chromosome behavior during meiosis in the F_1s was normal, i.e., the frequency of occasional irregularities was no higher than what was found in intervarietal hybrids within O. sativa. The F_1 plants were partially to completely fertile. It was concluded by the author that O. sativa var. fatua and O. sativa var. formosana are botanical varieties of O. sativa but O. balunga should be recognized as a separate, though very closely related, species

because of the distinct differences in morphology and growth habit.

Chromosome behavior during meiosis in the F_1 hybrids between O. sativa and the two forms of O. perennis was found to be essentially normal but the hybrids were completely or almost completely sterile. Similar results were obtained from a cross between O. sativa var. formosana and O. perennis (Cuban form). The author concluded that O. perennis is a distinct species from O. sativa but there is a relatively close relationship between the two.

The similar results obtained from crosses of O. sativa with both the American and the African forms, cubensis and barthii, of O. perennis plus the normal chromosome behavior and complete fertility found in hybrids between cubensis and barthii confirm the classification suggested by Chevalier (1932) placing these two forms in the same species, O. perennis. The author adopts O. perennis var. cubensis and O. perennis var. barthii as designations for the American and African forms, respectively.

Seven crosses involving five varieties of O. sativa and three varieties of O. glaberrima were made and studied. High frequencies of irregularities in chromosome behavior during meiosis were observed in all crosses and all F_1 plants were completely sterile. It was concluded that O. glaberrima is no doubt a distinct species from O. sativa and the cytogenetic relationship between these two species is more distant than that between O. sativa and O. balunga or O. perennis.

Similar results were obtained from cytogenetic studies of the crosses O. glaberrima X O. balunga, O. breviligulata X O. sativa and O. sativa X O. stapfii. These indirect results confirm the extremely close kinship between O. sativa and O. balunga and the very close relationships between O. glaberrima and the other two African forms, O. breviligulata and O. stapfii, which was pointed out by Chevalier (1932) and was also proved by direct cytogenetic evidence found in hybrids between O. glaberrima and O. breviligulata and between O. glaberrima and O. stapfii in the present research.

In spite of the very close cytogenetic relationship between O. glaberrima and O. breviligulata, however, the author agrees with earlier classifications that O. breviligulata should be recognized as a separate species from O. glaberrima on the ground of distinct morphological differences.

A still more distant relationship was found between O. sativa and O. officinalis from the studies. The cross was rather difficult to make and the viability of the F_1 plants was low. Although the only F_1 plant available for the study happened to be a triploid, the disturbed chromosome behavior and complete sterility agree with earlier findings in this type of hybrid. There is no doubt that O. officinalis is a distinct species and the cytogenetic relationship between this species and O. sativa is quite distant.

Based on cytogenetic evidence obtained in the present research, an analysis of the genomes in Oryza was attempted and

designations for genomes in the 10 forms included in this dissertation were given. O. sativa, O. sativa var. fatua, O. sativa var. formosana and O. balunga were considered to contain the same genome, A_1. O. perennis var. cubensis and O. perennis var. barthii were considered to possess basically the same genome as in O. sativa but somewhat differentiated. It is designated as A_2. The genome contained in O. glaberrima, O. breviligulata and O. stapfii is identical but different from A_1 or A_2 and was designated as E. The genome constitution of O. officinalis is concluded to be distinct from A or E, but the proper designation has to await further cytogenetic studies in hybrids of this species with other forms in Oryza.

Two probable paths through which O. sativa evolved in South East Asia are proposed. (1) O. sativa was derived directly from O. balunga. (2) O. sativa was derived indirectly from O. balunga with O. sativa var. formosana or/and O. sativa var. fatua as the immediate progenitors. Earlier theories on the origin of O. sativa were discussed.

Cytogenetic evidence obtained from the studies agrees with Chevalier's (1932) opinion that O. glaberrima was probably derived from O. breviligulata and is indigenous to tropical West Africa.

REFERENCES

Backer, C.A. 1946. The wild species of Oryza in the Malay Archipelago. Blumea Suppl. III: 45-55.

Burkill, I.H. 1935. DICTIONARY OF ECONOMIC PRODUCTS OF MALAY PENINSULA. vol. II. Crown Agents for the Colonies, London.

Capinpin, J.M. and A.B. Magnaye. 1951. Hybridization of cultivated and wild rices. Philip. Agric. 34: 219-229.

Chatterjee, D. 1947. Botany of the wild and cultivated rices. Nature, 160: 234-237.

_____. 1948. A modified key and enumeration of the species of Oryza Linn. Ind. J. Agric. Sci. 18: 185-192.

_____. 1951. Note on the origin and distribution of wild and cultivated rices. Ind. J. Genet. Pl. Breed. 11: 18-22.

Chevalier, A. 1910. Le riz sauvage de l'Afrique tropicale. Bull. Mus. Hist. Paris, 16: 404-408.

_____. 1932. Nouvelle contribution a l'etude systematique des Oryza. Rev. Bot. Appl. 12: 1014-1032.

_____. 1951. Un nouvelle espece d'Oryza sauvage d'Afrique tropicale. Rev. Bot. Appl. 31: 378-382.

_____. and O. Roehrich. 1914. Sur l'origine botanique des riz cultives. Compt. Rendu Acad. Sci. Paris, CLIX: 560-562.

Darlington, C.D. and A.P. Wylie. 1956. CHROMOSOME ATLAS OF FLOWERING PLANTS. George Allen & Unwin.

Dobzhansky, T. 1951. GENETICS AND THE ORIGIN OF SPECIES. 3rd ed. New York: Columbia University Press.

Ghose, R.L.M., M.B. Ghatge and V. Subrahmanyam. 1956. RICE IN INDIA. New Delhi: Ind. Council Agri. Res.

Gotoh, K. and E. Okura. 1933. A preliminary note on cytological studies of Oryza. J. Soc. Trop. Agri. Formosa, 5: 362-364.

Gotoh, K. and E. Okura. 1935. Cytological and genetical studies of Oryza. Jap. J. Genet. 11: 130-131.

Hara, S. 1942. Genetical studies on the wild rice in Formosa. Jap. J. Genet. 18: 183-184.

Hirayoshi, I. 1937. Species hybrids between cultivated rice and wild rice (Oryza latifolia) with special reference to their sterility and maturation division (A preliminary note). Jap. J. Genet. 13: 59-60.

Hitchcock, A.S. 1936. MANUAL OF THE GRASSES OF THE WEST INDIES. Washington: U.S.Government Printing Office.

Hooker, J.D. and B.D. Jackson. 1895. INDEX KEWENSIS. vol. II. Oxford: The Clarendon Press.

Hutchinson, J.B. and K. Ramiah. 1938. The description of crop plant characters and their range of variation II. Variability in rice. Ind. J. Agric. Sci. 8: 529-616.

Jones, J.W. and A.F. Longley. 1941. Sterility and aberrant chromosome numbers in Caloro and other varieties of rice. J. Agric. Res. 62: 381-401.

Krishnaswamy, N., V.S. Raman, B.V. Shetty and P. Chandrasekharan. 1954. Chromosome number of some Indian economic plants. Curr. Sci. 23: 64.

Kuang, H. 1951. Studies in rice cytology and genetics as well as breeding work in China. Agron. J. 43: 387-397.

Kuwada, Y. 1910. A cytological study of Oryza sativa. Bot. Mag. Tokyo, 24: 267-281.

Leon, H. 1946. FLORA DE CUBA. vol. I. Havana, Cuba: Cultural, S.A.

Mangelsdorf, P.C. 1952. Evolution under domestication. Amer. Nat. 86: 65-77.

Mitra, S.K. and P.M. Ganguli. 1932. Some observations on the characters of wild rice hybrids. Ind. J. Agri. Sci. 2: 271-279.

Morinaga, T. 1940. Cytological studies on O. sativa IV. The cytogenetics of F_1 hybrid of O. sativa L. and O. minuta Presl. Jap. J. Bot. 11: 1-16.

Morinaga, T. 1941. Cytological studies on O. sativa V. The cytogenetics of F_1 hybrid of O. sativa L. and O. latifolia Desv. Jap. J. Bot. 11: 461-478.

_____. 1943. Cytological studies on O. sativa VI. The cytogenetics of F_1 hybrid of O. minuta Presl. and O. latifolia Desv. Jap. J. Bot. 12: 347-357.

_____. 1956. Chromosome pairing at meiosis in F_1 hybrids and genomic constitution of Oryza. Reprinted from Exhibits, International Genetics Symposia, 1956, Sept. 6-12, Tokyo and Kyoto, Science Council of Japan.

_____. and M. Aoki. 1938. On the microsporogenesis of various interspecific rice hybrids in Oryza. Agri. and Hort. 13: 1993-2005 (in Japanese). Pl. Breed. Abs. 8, No. 1024.

_____. and H. Kuriyama. 1957. Cytological studies on Oryza sativa IX. The F_1 hybrid of O. sativa and O. glaberrima. Jap. J. Breed. 7: 57-65(in Japanese).

Nagai, I. 1959. JAPONICA RICE. ITS BREEDING AND CULTURE. Tokyo: Yokendo Ltd.

Nandi, H. K. 1936. Cytological investigations of rice varieties. Cytologia, 8: 277-305.

_____. 1937. The chromosome morphology, secondary association and origin of cultivated rice. J. Genet. 33: 315-336.

_____. 1938. Interspecific hybridization in Oryzeae I: Cytogenetical evidence of the hybrid origin of O. minuta. Trans. Bose Res. Inst., Calcuta, 11: 99-121.

Okura, E. 1913. Cytogenetical studies on Oryza. A preliminary note on interspecific hybrid between O. sativa L. and O. minuta Presl. Jap. J. Genet. 13: 212-214.

Pathak, G.N. 1940. Studies in the cytology of cereals. J. Genet. 39: 437-467.

Parthasarthy, N. 1938. Cytogenetical studies in Oryzeae and Phalaridae II: Further studies in Oryza. Cytologia, 9: 307-318.

_____. 1939. Cytological studies in Oryzeae and Phalaridae. Ann. Bot. N.S., 3: 43-76.

Porteres, R. 1956. Taxonome agrobotanique des riz cultives O. sativa Linne et O. glaberrima Steudel. J. d'Agri. trop. et de Bot. Appl. III(7-8): 341-856.

Prain, D. 1903. BENGAL PLANTS. vol. II. Calcutta.

Ramanujam, S. 1937. Cytogenetical studies in the Oryzeae III: Cytogenetical behavior of an interspecific hybrid in Oryza. J. Genet. 35: 223-258.

_____. 1938. Cytogenetical studies in the Oryzeae I: Chromosome studies in Oryza. Ann. Bot. N.S., 2: 107-126.

Ramiah, K. 1928. Artificial hybridization in rice. Agri. J. Ind. 22: 17-23.

_____. and R.L.M. Ghose. 1951. Origin and distribution of cultivated plants of south Asia--Rice. Ind. J. Genet. Pl. Breed. 11: 7-13.

_____. and M.B.V.N. Rao. 1953. RICE BREEDING AND GENETICS. The Indian Council of Agricultural Research.

Roschevicz, R.J. 1931. A contribution to the knowledge of rice. Bull. Appl. Bot. Genet. Pl. Breed. 27(4): 1-133. English summary: 119-133.

Roy, S.H. 1921. A preliminary classification of the wild rices of the central Provinces and Berar. Agri. J. Ind. 16: 365-380.

Sampath, S. and K. Ramanathan. 1949. Chromosome numbers in Indian economic plants---III. Curr. Sci. 18: 408.

Sampath, S. and M.B.V.N. Rao. 1951. Interrelationships between species in the genus Oryza. Ind. J. Genet. Pl. Breed. 11: 14-17.

_____. and S. Govindaswami. 1958. Wild rice of Orissa--- Their relationship to cultivated varieties. Rice News Teller, 6(3): 17-20.

Sax, K. 1935. The cytological analysis of species-hybrids. Bot. Rev. 1: 100-117.

Selim, A.G. 1930-31. A cytological study of Oryza sativa L. Cytologia, 2: 1-26.

Shama Rao and H.K.R. Seetharaman. 1955. An interspecific hybrid in Oryza. Curr. Sci. 24: 346-347.

Stebbins Jr., G.L. 1945. The cytological analysis of species hybrids. II. Bot. Rev. 11: 463-486.

_____. 1950. VARIATION AND EVOLUTION IN PLANTS. New York: Columbia University Press.

_____. 1958. The inviability, weakness and sterility of interspecific hybrids. Adv. Genet. 9: 147-203. Acad. Press, Inc., N.Y.

Stephens, S.G. 1947. Cytogenetics of Gossypium and the problem of the New World cottons. Adv. Genet. 1: 431-442. Acad. Press, Inc., N.Y.

Suzuki, S. and G. Masamune. 1935. A new wild species of rice plant in Taiwan. Oryza formosana Masamune et Suzuki. Trans. Nat. Hist. Soc. Formosa, XXV, 144, p.320.

Suzuki, S. 1935. On the wild rice of Taiwan. Jap. Acad. Assoc. Rep. 10(1): 161-165 (in Japanese).

Ting, Y. 1933(a). Wild rice of Kwantung and new strains bred by hybridization. J. Agri. Assoc. China, 114: 204-217.

_____. 1933(b). Origination of the rice cultivation in China. Coll. Agri. Sun Yat Sen Univ. Publ. series III, Agron. Bull. No. 7.

Vavilov, N.I. 1926. Studies on the origin of cultivated plants. Bull. Appl. Bot. 16: 1-248.

_____. 1951. THE ORIGIN, VARIATION, IMMUNITY AND BREEDING OF CULTIVATED PLANTS. Chron. Bot. 13: 1-334., Waltham, Mass., Chronica Botanica Co.

Watt, G. 1891. DICTIONARY OF THE ECONOMIC PRODUCTS OF INDIA. vol. V. London.

Yao, S.Y., M.T. Henderson and N.E. Jodon. 1958. Cryptic structural hybridity as a probable cause of sterility in intervarietal hybrids of cultivated rice, Oryza sativa L. Cytologia, 23(1): 46-55.

AUTOBIOGRAPHY

Birdie Pu-sheng Yeh was born in Hankow, China, May 7, 1927. She entered National Wu-han University in 1947, majoring in Agronomy. She moved to Taiwan in 1948 and transferred to National Taiwan University in 1949 as a sophomore majoring in Agronomy.

She received the Bachelor of Science degree from that University in 1951.

She worked for four and one half years as teaching assistant in plant breeding in the Agronomy Department of National Taiwan University.

She entered the Graduate School of Louisiana State University in September, 1956 and received the Master of Science degree from that University in February, 1958.

She is now a candidate for the degree of Doctor of Philosophy in the Department of Agronomy.

EXAMINATION AND THESIS REPORT

Candidate: Birdie Pu-Sheng Yeh

Major Field: Agronomy

Title of Thesis: Cytogenetic Relationships between Cultivated Rice and other Diploid Species of Oryza.

Approved:

M. T. Henderson
Major Professor and Chairman

Richard J. Russell
Dean of the Graduate School

EXAMINING COMMITTEE:

E A Fieger

J R Kreig

H C Rhoades

Lewis H. Flint

M. B. Sturgis

Date of Examination:

May 19, 1960